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Vol. 71, No. 2 April 1973

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SCIENTIFIC ADVICE ON CATCH LEVELS

J. A. GULLAND AND L. K. BOEREMA[1]

ABSTRACT

The sustainable yield, or maximum sustainable yield, has been used to provide, on an objective scientific basis, target figures for the catches to be taken from a heavily exploited stock that is under regulation. The simple concept of sustainable yield does not, however, provide a completely adequate guide when the biological system is complex. Certain other quantities—the replacement yield, the sustainable yield from a stock in equilibrium, the maintainable yield, and the catch for desired harvesting rate—are defined which correspond more closely to the biological reality.

One or other of these will provide a better guide for management, depending on the nature of the divergence from the simple model. In whale populations the major divergence is the lag between changes in adult stock and changes in recruitment; replacement yield or maintainable yield are the most useful. In many fish stocks, fluctuations in year-class strength are more important: catch for desired harvesting rate may be better.

Various fishing research organizations are concerned with the setting of annual catch quotas or other measures for the management of the resources which are their responsibility. Agreement on the level of these quotas is more easily reached if they are determined by objective scientific criteria. Apart from the continuing difficulty in making precise assessments concerning any wild animals, this guidance is difficult to provide without some agreed basis on how the "correct" catch should be calculated.

At present there is not a single theoretical model for determining this catch that combines all the desirable features of (a) being readily understandable (at least in general outline) to the decision makers, (b) describing and predicting in a realistic manner, and to an acceptable degree of precision the events in every fish stock to which it may need to be applied, and (c) capable of being applied to a specific fishery without great demands in data and analysis. The models associated with Schaefer (1954) on the one hand and with Ricker (1958) and Beverton and Holt (1957) (in the simple form when no account is taken of fishery-induced changes in recruitment) on the other fail, for many important fisheries, to satisfy the second criterion. The density-dependent form of the Ricker-Beverton Holt approach is more satisfactory in this regard, but makes heavy demands on data and analysis. Despite these difficulties, and in the absence of a single uniformly acceptable model, some objective guidance can be given on the magnitude of the catches that can be taken from heavily exploited stocks, and such guidance is being used by many regional commissions [e.g., IWC (International Whaling Commission), Inter-American Tropical Tuna Commission, ICNAF (International Commission for the Northwest Atlantic Fisheries)] in framing regulations. This paper explores some of the bases of such guidance, in the hope of facilitating the future preparation of advice on desirable catch levels.

SUSTAINABLE YIELD

The concept of a sustainable yield as often applied in practice, and more particularly the idea of the maximum sustainable yield, is based on a simplified model of a natural animal population in which the population is treated as a single unit, ignoring the fact that there are individuals of different ages, etc.; it also ignores all disturbing influences on the population, other than removals by man. If such a population has been reduced below the limiting carrying

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capacity of its environment, it will tend to increase. In the simplified case the rate of increase will depend solely on the abundance of the population (or the abundance of the exploitable part of the population).

On the basis of this simple model, it is clear that if the annual removals by man (catch) are equal to the annual natural increase, the size of the population will remain unaltered, and such a catch can be sustained indefinitely. For such a situation the sustainable yield can be defined as being equal to the net rate of natural increase and represents the yield which can be maintained indefinitely while also maintaining the stock size at the same level.

The rate of increase, as a proportion of the population, generally decreases as the population increases. The absolute value of this natural increase, and hence the sustainable yield, is small for very small populations and is also small for large populations as they approach the limiting value. It will be greatest for some intermediate level of population which is the population abundance giving the maximum sustainable yield (MSY) (see Figure 1).

If the population is less than the level giving the MSY, no catch greater than the sustainable yield can be maintained for more than a short time. The population will be reduced each year by an amount approximately equal to the difference between the catch and the sustainable yield. The sustainable yield will in turn be reduced, leading to an ever faster reduction, which, if the amount caught is maintained by fishing harder and harder, will in a fairly short time lead to the "commercial extinction" of the stock.

On the other hand, if the population is above the MSY level, catches greater than the sustainable yield corresponding to that population level, can be maintained indefinitely, provided that they are not greater than the MSY. This is because, as these catches reduce the population toward the MSY level, the sustainable yield will increase. When the population is reduced to the level at which the sustainable yield is equal to the catch, then the catch can be maintained indefinitely without further change. The maintainable yield may then be defined as the largest catch that can be maintained from the population, at whatever level of stock size, over an indefinite period. It will be identical to the sustainable yield for populations below the level giving the MSY, and it will be equal to the MSY for population at or above this level. In the latter case harvesting the maintainable yield will involve for a short transitional period a change in population abundance as it is thinned out to the MSY level.

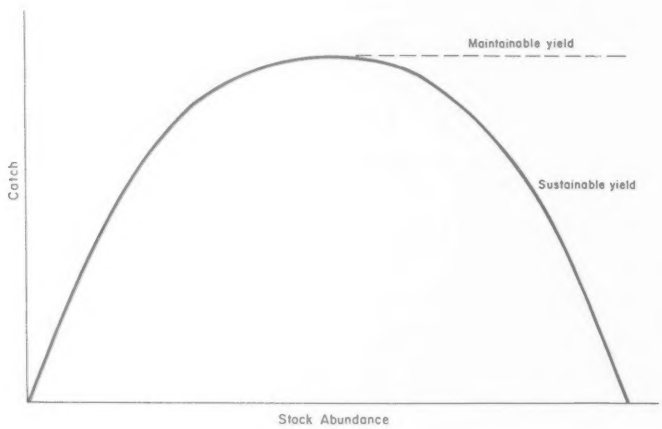

FIGURE 1.—Sustainable yield and maintainable yield as function of stock abundance.

The simplified description above does not in fact fit precisely the actual situation in the sea. Two main divergences may be mentioned: 1) the fact that the net rate of natural increase will depend on past events as well as on the current abundance and 2) there are many sources of variation, other than exploitation, in the abundance of populations. The most important of these for many fish species of commercial importance is natural fluctuations, especially in recruitment, caused by variations in environmental conditioning. Other causes of variation, e.g., changes in the availability or distribution of fish, will have significant effects on the success or otherwise of the fishery in a particular season, but will not be discussed here. The first of these is particularly significant for whales, and the second for some fish populations, especially in temperate and subarctic waters.

LAG EFFECTS

For whales, the net rate of natural increase in the exploitable part of the population is usually expressed in numbers and is the difference between the number of animals dying from natural (nonfishery) causes, which will be some fairly constant proportion of the number in the current stock, and the numbers of recruits entering the exploitable stock, which will be closely proportional to the numbers of mature animals alive some years previously, at least at small to moderate population sizes. As the population approaches its equilibrium, unexploited level, the recruits will be less, or the mortality more, or both, than expected from a purely proportional relationship with population abundance. If the abundance of the stock is changing, the concept of a sustainable yield becomes complicated. If, for example, the stock has recently been reduced, then the recruits during the year will have come from a parent population that is greater than the current mature stock. The number of recruits may then be appreciably greater than the number of natural deaths, so that quite a large catch could be taken and still leave the population at the end of the year the same size that it was in the beginning. However, such a catch could not be sustained indefinitely, since the number of recruits in later years will decrease. For such a stock a number of different terms may need to be defined.

The replacement yield for a given year is the catch which, if taken, will leave the abundance of the exploitable part of the population at the end of the year the same as at the beginning. This is specific to a particular year and includes no concept of continuity. Even if the replacement yield is taken in one year, it is unlikely that the replacement yield in the following year will be the same, unless this population has remained at around the same abundance for some time (not less than the time span between birth and recruitment).

The simple definition of the sustainable yield refers to an equilibrium situation and cannot strictly be used in a situation of changing stock size. When the population has been changing it may be convenient to define the (equivalent) sustainable yield as the sustainable yield from a population of the same abundance (or with the same abundance of the exploited phase), which has remained at this level of abundance for a long time. It is the value that would be obtained from reading off the yield corresponding to the abundance in a figure such as Figure 1. Hence if the catch taken is set equal to this sustainable yield, the population abundance will not, in general, remain unaltered.

It is evident that if the stock (or its exploitable phase) has recently been decreasing, and, as in the case of whales, the recruits are roughly proportional to the abundance of an earlier and larger parent stock, the replacement yield is greater than the sustainable yield of the present stock size. If, on the other hand, the stock has recently been increasing, the replacement yield is equal to the difference between the recruitment from a smaller parent stock and the natural mortality of the greater present stock and may therefore be lower than the sustainable yield of either the parent stock size or the present stock size.

In a situation in which the stock is above the level of maximum sustainable yield, the maintainable yield, as defined above, which is equal to the maximum sustainable yield, is not affected by recent changes in stock size. If the

stock is changing and is below the level of MSY, however, the maintainable yield is equal neither to the replacement yield nor to the sustainable yield corresponding to the abundance of either parent or present stock, but will be at a level between the sustainable yields of these two stock sizes. Maintenance of the catch at the level of maintainable yield will ultimately lead to an equilibrium situation with a stock size in between the original "parent" and "present" stock sizes.

It should be noted that if the stocks are below MSY level and have recently been decreasing, the maintainable yield is lower than the replacement yield, whereas if the stocks have recently been increasing, the maintainable yield is the higher of the two. Any catch lower than the maintainable yield, if kept at the same level for a sufficient period of time, will ultimately lead to a rebuilding of the stocks, even though in the short term it may cause some decrease.

If the population is below the MSY level, setting the catch equal to the estimated sustainable yield will, as has been frequently pointed out, lead to an unstable situation. If the estimate used is only just too high the stock will start to decline, the gap between the catch and the actual sustainable yield will widen at an accelerating rate, and the stock will decline ever more rapidly until the catch is adjusted. As pointed out by Y. Fukuda (pers. comm.) this can occur, if there are natural fluctuations, even if the catch taken is exactly equal to the sustainable yield under average conditions. Suppose, for example, there is a poor year for reproduction, leading to reduced recruitment. Then the catch, if unchanged, will reduce the stock, and this reduced stock will have a smaller sustainable yield, even under average conditions. A fixed catch will then continue to deplete the stock at an accelerating rate. Similarly, a favorable if transient fluctuation and a fixed catch will result in a continuous increase in population to above the MSY level.

The significance of the differences among the various terms can perhaps best be illustrated with some hypothetical examples of different actions which might have been taken after the serious decline in the fin whale stocks in the late 1950's and early 1960's. For simplicity, it has been assumed that the stocks have been declining by 10,000 whales per year from a level of 120,000 in 1960 to 70,000 in 1965, figures which are roughly similar to the decline as estimated by the Scientific Committee of the IWC. Recruitment rate has been taken for the purpose of this example at 8%, recruitment age at 5 years, and natural mortality rate at 4%, which values were assumed to remain constant within the range of stock sizes of the examples (see Table 1).

TABLE 1.—Trends in population and catch of Antarctic fin whales, if, after 1965, catches were set equal to the replacement yield, or to the sustainable yield. (Thousands of animals.)

	Catch = replacement yield				Catch = sustainable yield			
Year	Stock	N[1]	R[2]	Catch	Stock	N[1]	R[2]	Catch
1960	120				120			
1961	110				110			
1962	100				100			
1963	90				90			
1964	80				80			
1965	70	2.80	9.60	6.80	70	2.80	9.60	2.80
1966	70	2.80	8.80	6.00	74.0	2.96	8.80	2.96
1967	70	2.80	8.00	5.20	76.88	3.08	8.00	3.08
1968	70	2.80	7.20	4.40	78.72	3.15	7.20	3.15
1969	70	2.80	6.40	3.60	79.62	3.18	6.40	3.18
1970	70	2.80	5.60	2.80	79.66	3.19	5.60	3.19
1971	70	2.80	5.60	2.80	78.88	3.16	5.92	3.16
1972	70	2.80	5.60	2.80	78.48	3.14	6.18	3.14

[1] N = numbers dying from natural causes = 4% of current stock.
[2] R = numbers of recruits = 8% of adult stock 5 years earlier.

If from 1965 onward, catch quotas had been introduced equal to the replacement yield, the stock would have been maintained at the level of 70,000 whales, and the quota would have been 6,800 whales in 1965, declining by 800 per year to 2,800 whales in 1970, after which the number would have remained at this level.

If, on the other hand, the sustainable yield had been taken every year the catch quota would have been 2,800 in 1965, slowly rising to 3,190 in 1970, then declining to 3,130 in 1973 and stabilizing at about 3,140 thereafter, at which time the stock size would practically have stabilized at 78,560 whales.

The highest constant annual yield which could have been taken from 1965 onward—the maintainable yield—would have been about 3,125 whales, which would have led to a stock size of about 78,200 whales by the mid-1970's (Figure 2a).

For the purpose of demonstrating the effect of increasing stock size, the effects of different catch quotas have been calculated for the situation in which the stock has risen from 70,000 to 80,000 whales over a 5-year period (say, from 1965 to 1970) by 2,000 whales per year. Catch quota equal to the replacement yield, which would maintain the stocks at 80,000 whales, would have been 2,400 whales in 1970, increasing by 160 whales per year to 3,200 whales in 1975, after which the figure would remain constant.

If the sustainable yield had been taken, the catch quota in 1970 would have been 3,200 whales, decreasing to 3,120 in 1974 and thereafter stabilizing at around 3,130, and a stock size of around 78,310 whales.

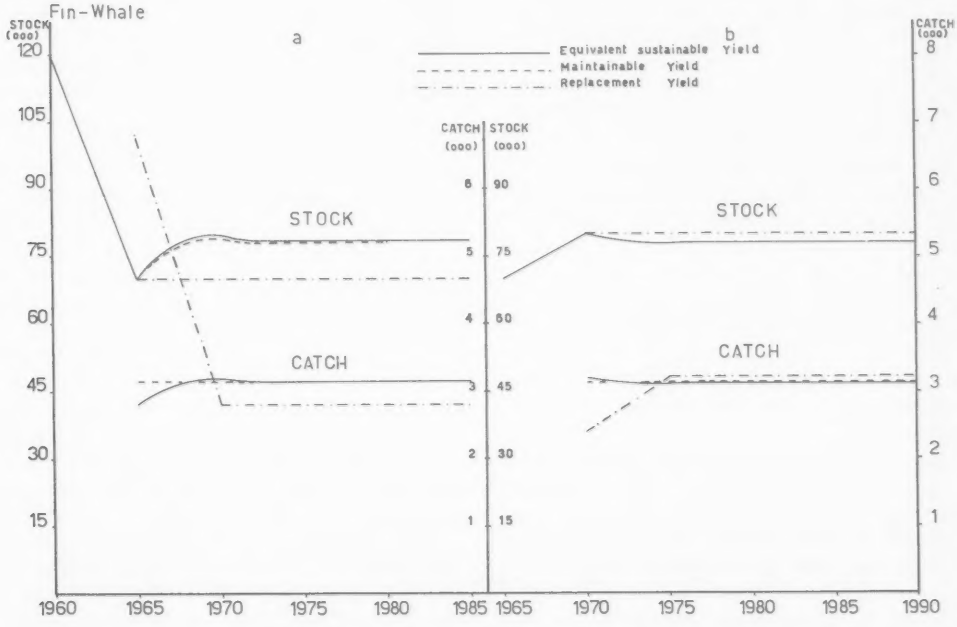

FIGURE 2.—Examples of catch level and stock size resulting from regulating catches of fin whales at the level of equivalent sustainable yield, maintainable yield, and replacement yield respectively, in the case that the regulations were introduced a) after a constant decline in the stock (in the example assumed to have taken place from 1960 till 1965) and b) after a constant increase in the stock size (in the example assumed to have taken place from 1965 till 1970). Parameters used in these models are specified in the text.

The maintainable yield would in this case have been 3,134 whales, leading to a stock size of about 78,360 whales in the later 1970's (Figure 2b).

These examples demonstrate some general features. Firstly, they show that catch regulations based on replacement yield, equivalent sustainable yield or maintainable yield will all lead to an equilibrium situation in which the stock size and permitted catch reach a stable level. In the case in which the stock has recently been changing, regulation based on replacement yield will maintain the stock at the level at which it was at the start of this regulation, but catches regulated at the level of sustainable yield or of maintainable yield will lead to a different stock level. If the stock had recently been declining, the long-range stock level and yield would then be rather higher than that based on taking the replacement yield, and if the stocks had recently been decreasing, the long-range equilibrium would be reached at a somewhat lower stock size. Although there are some differences in catch level between regulations based on sustainable yield and on maintainable yield in the first years after introduction, the long-term effects of these two criteria for regulation are very similar.

It would thus seem that replacement yield, which maintains the stock at the same level, but requires changing quotas in the first years, and maintainable yield, which is the highest catch that can be maintained indefinitely from the stock size available, but will lead to a change in stock size in the first years, will provide the best guide for whaling management decisions in situations in which stock sizes have recently been changing.

Any scientific advice on these matters should be clearly defined. Part of recent confusion about frequently changing estimates of permissible yield by the Scientific Committee of the IWC has been due to insufficient definition of the terminology as outlined above.

Finally, it may be noted, from the arguments given above, that the rate of increase of population depleted well below its level of MSY, but completely protected thereafter, is less than the net recruitment rate in an equilibrium situation. For example, for recruitment rate 8%, recruitment age 5 years, and natural mortality rate 4%, the net recruitment rate in equilibrium situation is 4%, but the rate of increase in recovering, unfished, population in any year would be about 3% of the stock size in that year, or about 3.5% of the size of the parent stock (the stock size 5 years earlier).

NATURAL FLUCTUATIONS

For fish, on the other hand, the lag effects on the average are less disruptive to the simple model than natural fluctuations, among which changes in year-class strength are the most striking. Where differences in year classes are very large, it is likely that when a strong year class enters the fishery the stock will increase whatever catch is taken (within practicable limits); when a succession of strong year classes is replaced by a run of poor ones, the stock may decrease even if fishing is cut back virtually to nothing. In this situation it is difficult to talk about a sustainable or maintainable yield.

However, it is precisely in the situation of a declining stock, when strong year classes are being replaced by weak ones, that concern about the management of the stock is likely to be greatest, and when scientists are often asked for advice (e.g., regarding herring in subarea 5 of ICNAF). Sometimes the advice is requested in general terms, allowing the scientists to describe the situation in detail, but leaving the decision as to the control measures (such as the level of catch quotas) to administrators. At other times the administrators cannot decide easily among themselves on the amount of catch that should be taken and ask the scientists for an explicit figure of the "correct" or "desirable" catch. This requires some objective basis for determining this, analogous to the sustainable or replacement yield for whales.

The simplest case is that in which the abundance of recruits (strength of the year class) is independent of the abundance of the parent stock. All that management can do is make the best use of whatever recruitment happened to occur, that is, to maintain fishing at whatever level is considered the optimum position on the yield-per-recruit curve. In the simplest situation the curve of yield per recruit

as a function of fishing effort will have a clear maximum, for which the corresponding fishing mortality can be reasonably easily determined. This fishing mortality might then be considered as being one possible value of the optimum fishing mortality. However, in practice the yield curve will be quite flat in the neighborhood of the maximum. This may make determination of the position of the maximum difficult and will certainly mean that obtaining the absolute maximum (e.g., moving from the effort giving 99% of the catch to that giving 100%) will require a disproportionate increase in effort and hence in costs (Gulland, 1968a). Given particular values of the price of fish and costs of exerting unit fishing mortality, a mortality which will maximize the net economic yield can be calculated, and might be considered the optimum for the given economic situation. Different economic conditions will result in somewhat different optima, but for most conditions the optimum will lie within a fairly narrow range. It is, therefore, possible to define a target of the desirable fishing mortality in the middle of this range which will receive general acceptance, or at least, especially for a heavily fished stock, a minimum target at the upper end of this range. Whatever the precise objectives and economic conditions of any individual country participating in a fishery, the reduction of the amount of fishing to this target level should be desirable.

A more objective method of calculating a limiting value to desirable fishing mortality may be derived from considering the marginal yield, i.e., the increase in total yield achieved by adding one extra unit of effort (Gulland, 1968b). The marginal yield will be equal to the slope of the tangent to the curve of catch against fishing effort. It will always be less than the catch per unit effort, which is the slope of the line joining the point in the curve to the origin. The economic optimum, i.e., the greatest net economic return, occurs when the value of the marginal yield is equal to the marginal costs of a unit of effort. At the point giving the maximum physical yield the marginal yield will be zero. Clearly from any practical viewpoint, it would be undesirable to increase the amount of fishing beyond the level at which the value of the marginal yield is small compared with the costs of the extra unit of effort required to produce that yield. The question then arises as to what might be considered as small. An arbitrary figure, which has in fact been used in connection with the herring on Georges Bank (ICNAF, 1972) is a marginal yield equal to one-tenth of the original catch per unit effort in the very lightly exploited fishery. This is illustrated in Figure 3. The two straight lines through the origin show catches per unit effort

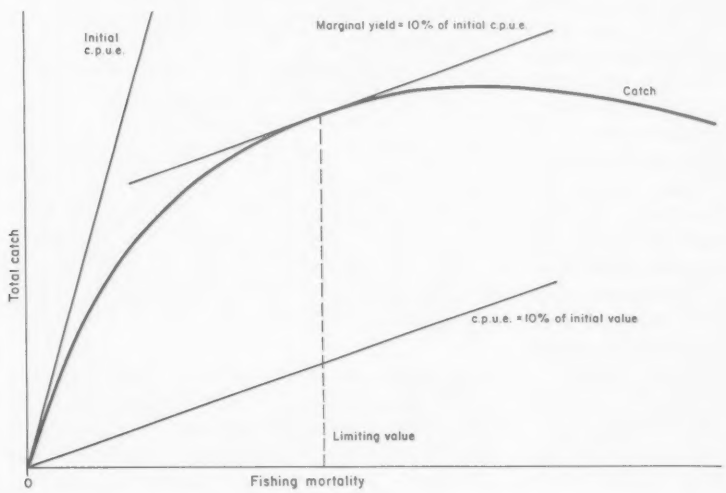

FIGURE 3.—Determination of an economic optimum position at which the marginal yield is 10% of the initial catch per unit effort.

in the nearly unexploited fishery—the tangent to the catch curve at the origin—and a catch per unit effort of 10% of this value. The limiting point beyond which any increase in fishing would certainly not be worthwhile—assuming a marginal yield of 10% of the initial catch per unit effort is not worthwhile—is where the tangent to curve is parallel to this 10% line. The selection of 10% is arbitrary but once the 10% figure is accepted the corresponding catch can be calculated objectively. Thus it can be used to provide a Commission or other management body objective guidance based on scientific grounds.

Unless there are marked density-dependent changes in mortality or growth this target will be achieved by exerting some fixed rate of fishing mortality. It may be noted that the optimum fishing mortality, exerted at a constant rate during the whole of its life, above the age at first capture, is the same for any strength of year class, but slightly larger catches would in principle be obtained by fishing less hard when the fish are young, and harder when they are old, i.e., concentrating catches more at the age when the total biomass of the year class is at its maximum. The fishing mortality in a particular year which leads to the greatest catch over a period will be the mean of the best mortality for each year class present, weighted according to their strengths. If the year classes are equal, this will be equal to the optimum constant rate for a single year class during its entire life. If there is a big variation in year-class strength there would be some theoretical advantage, other things being equal, in fishing slightly harder when the strongest year class present is middle-aged (since they will not grow much more but will suffer losses by natural mortality), and less hard when the strong year classes have just recruited. However, the theoretical increases in yield are not likely to be great, and it is simpler to keep, as the objective, the same constant fishing mortality independent of year-class change. From an economic standpoint the optimum level of fishing mortality will increase slightly when strong year classes are present, because then it becomes more worthwhile to squeeze out an extra 1 or 2% of the maximum yield. For those few fisheries for which the investigators are fortunate enough to have immediately available a measure of total effort which provides a measure of fishing mortality consistent from year to year, the optimum level of fishing can be defined at once in terms of total fishing effort, without the need for year to year adjustments.

Usually difficulties of standardization in a multinational or multigear fishery, or changes in the effectiveness of a nominal unit of effort, will mean that the amount of fishing in each year will have to be controlled in terms of total catch. The scientists can, in principle, given adequate information, calculate what the magnitude of this catch should be, taking into account the strength of the year classes already present in the fishery, and those that will be recruited during the year in question. This catch might be defined as the catch for optimum harvesting rate.

Often a precise optimum level of fishing mortality cannot be defined or cannot be agreed upon. It is still possible to estimate the catches in each year which would be required to attain any prescribed value of fishing mortality. These mortalities may be those which occurred at some previous time when it was believed that the fishery was in better condition (in some general, unspecified sense) than the present, or some convenient figure which the scientists believe approximates to the optimum condition. In this way the scientists, without preempting the administrators' duty to decide on the objective of management, can provide some figures derived in a reasonably objective way, on which it may be possible for agreement to be reached. An example of such calculations are those made by the Assessments Sub-Committee of ICNAF for the cod stock at West Greenland. This stock undergoes moderately strong year-class fluctuations, and estimates have been made of the catches required to attain fishing mortalities of 0.8 and 0.6, as set out in Table 2 (from ICNAF, 1970).

It may be noted that for virtually all patterns of mortality, there is a drop in predicted catch from 1969 to 1970 and again from 1970 to 1971, due to the entry of weak year classes into the fishery.

TABLE 2.—Catches (thousands of tons) of cod from the West Greenland stock in 1970 and 1971 corresponding to different values of fishing mortality (in parentheses).

1968	1969	1970	1971
382 (0.8)	225 (0.6)	178 (0.6)	159(0.6) 203(0.8)
		224 (0.8)	143(0.6) 182(0.8)

For most fish stocks there is a reasonable likelihood that changes in the abundance of the adult stock brought about by fishing will have some effect on the average level of recruitment, though the extent of such effects may not be known. When they are known, they can be incorporated into the calculations to obtain the catch rates corresponding to different objectives.

The management of salmon stocks generally corresponds to this situation. The relation between spawning stock (escapement) and subsequent recruitment is usually claimed to be known and has a maximum at some intermediate level of spawning stock. The catches are adjusted to obtain some desired level of escapement. This might be the level giving—under average conditions—the maximum recruitment, though a more nearly optimum strategy would be to take a rather larger catch, such that the immediate gain in increased catch would be more than the expected loss (with or without any discounting). In such a situation it is possible to define, purely on biological grounds, a catch for maximum recruitment; and also, using both biological and economic considerations, a catch for optimum spawning (or optimum escapement).[2]

The nature of the Pacific salmon fisheries—the movement of the prespawning fish through the fishing area during a short season and the spawning and subsequent death of all those not caught—makes relatively easy the visualization of the catches as defined here, since they are equal to the number of fish arriving at the fishing grounds, less the escapement required for maximum recruitment, or the optimum escapement respectively. However, the same definition could apply to any fishery, though in practice it can be applied only in those few fisheries for which the stock/recruit relationship is well known. It may be noted that these definitions lead to very great fluctuations in the catch that should be taken. Very large catches may be taken from good runs, but the allowable catch would fall to a very low level, or even zero, when the run is poor, and little, if at all, above the required escapement. The proportion of the stock (run) that is harvested decreases rapidly with decreasing run and falls to zero as soon as the size of the run drops to or below the target escapement.

Unfortunately, for most fisheries there is little firm information on the relation between adult stock and average recruitment. An obvious example of the resultant difficulties in defining objectively any specific catch quota is occurring for both the herring and haddock on Georges Bank (subarea 5 of ICNAF). For the haddock there has been an unprecedented run of poor year classes (those of 1964 to 1970 inclusive) which, combined with exceptionally heavy fishing in 1966 and 1967, has reduced the stock to a very low level. Though the more recent of the weak year classes (since about 1968) were associated with a low parent abundance, the earlier ones came from moderate to large stocks—in fact stocks of about the same abundance as those giving the very large year classes of 1962 and 1963. Thus although it is highly probable that the decline in adult stock is among the causes of the run of poor year classes, it is certainly not the only cause.

The ICNAF scientists have, therefore, pointed out that the sensible policy is to take action to

[2] This outline of the scientific rationale of salmon management ignores the great practical difficulties of management of any specific salmon fishery—the mixture at sea of fish from several different stocks, the difficulty of obtaining accurate measures of the incoming run before the start of the very short season, etc. These are outside the scope of the present note.

build up the spawning stock, since this will almost certainly increase the probability of future year classes being of average strength or better. However, there is no guarantee that, even if in the extreme case the catches are cut to zero, there will be any increase in recruitment compared with what would have occurred with unrestricted fishing.

This means that, since there is no good knowledge of the stock/recruit relation, there is no catch uniquely definable on scientific grounds as the best catch, though the optimum policy, for a stock at a low level, must lie between catching nothing (for the most rapid rebuilding of the adult stocks) and fishing at the rate which makes the best use of those fish which have, in fact, been recruited.

A catch that can be objectively defined, which will often lie in this range and which may also be a reasonable catch to take for the benefit of the fishery, is the replacement catch. This can be defined, in exactly the same way as before, as that catch which will ensure that the stock at the end of the year is the same as that at the beginning of the year. The stock in question could be the spawning stock, or the total fishable stock, and its magnitude could be expressed either as weight or numbers. (The use of numbers makes calculations easier and clearer.)

For example, recent reports of ICNAF's Assessment Sub-Committee have set out the changes in the numbers in the Georges Bank haddock stock, separating additions through recruitment, and removals by fishing and natural mortality. Thus during 1970 there were 16 million recruits, and some 3 million fish died through nonfishing causes, i.e., a net natural increase of 13 million fish, which was about twice the catch in numbers (ca. 5.3 million). However, because the deaths (through both fishing and natural cases) were mainly of large fish (average age in U.S. landings were 6.6 years of 2.4 kg weight), the deaths (in weight) were much larger than the weight of recruits, though this was almost balanced by the growth of the survivors. Thus the catch of 12,000 tons was about equal to the net natural additions, i.e., the catch was equal to the replacement catch, in weight, though less than the replacement catch in numbers.

The replacement catch varies very greatly. Thus between 1968 and 1969 when the natural deaths in the Georges Bank were 5 million fish and the recruits only 1 million, the stock, in numbers, could be maintained only by introducing 4 million fish onto the grounds, i.e., a replacement catch of minus 4 million fish. Conversely, when a very strong year class is recruited to the fishery, the replacement catch would be large and require a fishing effort well in excess of that giving the optimum mortality. The variation in the replacement catch, defined in terms of weight, will be less severe. Even so, it is clear that the replacement catch cannot be used blindly as the determinant for the catch to be taken in any particular season. It will, however, provide some sort of guide as to whether the proposed action will improve things (proposed catch is less than the replacement catch), or allow them to get worse. Unfortunately it is not a perfect guide. For example the average condition of the stock, over a period, will be maintained only if, when a strong year class is entering the fishery, the opportunity is taken to build up the stock to balance the occasions when poor year classes occur, i.e., less than the replacement catch should be taken when strong year classes are being recruited. Also, the practical application depends on obtaining good and early estimates of the strength of the incoming recruitment.

Regulations, such as catch quotas, based on a catch defined in terms of a particular harvesting rate would seem to form a better guide. Though the optimum mortality cannot be determined unless the form of the stock/recruit relation is known, an optimum rate (for any given economic or social policy) can be calculated on the assumption of constant recruitment. If the recruitment is affected by the abundance of the adult stock and the stock is at a low level, the optimum rate must be somewhat less. Therefore an upper bound can be set on the desirable level of catch. Further, various assumptions can be made concerning the form of the stock/recruit curve, and the corresponding relation between fishing mortality and total yield calculated. The scientific advice could then be presented in four columns: the first would list the possible objectives; the

second would give assumptions that could be made about the recruitment; the third and fourth columns would then give the fishing mortality necessary to achieve the objective and the corresponding catch in the forthcoming season. For example, for a purely hypothetical stock the information could be given as follows:

Objective and recruitment	*Optimum F*	*Catch* (tons)
Maximum physical yield:		
Constant	1.2	110,000
Moderately density-dependent	0.9	84,000
Strongly density-dependent	0.6	59,000
Maximum economic yield:[1]		
Constant	0.8	76,000
Moderately density-dependent	0.7	68,000
Strongly density-dependent	0.5	50,000

[1] For a certain set of assumptions on costs and prices.

While this still leaves a wide choice open—a range of over twofold, the more extreme values might be ignored so that the real choice may not be large, and the information provides a useful basis for determining management action.

REBUILDING DEPLETED STOCKS

A special problem arises when advising on the management of badly depleted stocks, especially one (e.g., of whales) in which recruitment is closely dependent on the abundance of the adult stock.

For such a stock calculations can be made of the replacement yield, or equivalent sustainable yield, but this should not imply that these are the proper objectives. Rather action should be taken to rebuild the stock. This is done most rapidly by cutting the catches to zero for a period. The optimum strategy between this (making the greatest present sacrifice for the maximum long-term benefit) and merely maintaining the situation (making no present sacrifice) will be determined by a number of factors, mainly economic. This will include the relative values placed on present and future catches, alternative employment for the excess men and equipment in the present fisheries, etc. For example, it would be much easier to stop for a period the offshore herring fishery on Georges Bank, since the vessels concerned can switch to other fisheries, than to do the same for Antarctic whales.

The general policy to be followed by the management body—to aim for the maximum physical yield from a given stock, or some lesser physical yield but with greater economic benefits, to rebuild a depleted stock quickly or merely prevent its further decline—must be determined by that body taking all factors into account and cannot be decided purely on biological grounds. What can be determined by objective scientific calculations is the actual procedure to be followed—specifically the catch to be taken in each season—to implement the chosen policy. This note has been concerned purely with a discussion of this second step.

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LITERATURE CITED

BEVERTON, R. J. H., AND S. J. HOLT
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G. B.) Ser. II, 19, 533 p.

GULLAND, J. A.
1968a. The concept of the maximum sustainable yield, and fishery management. FAO (Food Agric. Organ. U.N.) Fish. Tech. Pap. 70, 30 p.
1968b. The concept of the marginal yield from exploited fish stocks. J. Cons. 32:256-261.

INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES.
1970. Report of Assessment Sub-Committee to 1970 Annual Meeting. Int. Comm. Northwest Atl. Fish. Annu. Proc., p. 33-65.
1972. Report of Assessment Sub-Committee to 1972 Annual Meeting. Int. Comm. Northwest Atl. Fish. Annu. Proc., p. 17-42.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.

COMPARATIVE STUDY OF ADAPTATIONS FOR CONTINUOUS SWIMMING AND HYDROSTATIC EQUILIBRIUM OF SCOMBROID AND XIPHOID FISHES

JOHN J. MAGNUSON[1, 2]

ABSTRACT

Scombroid fishes swim continuously with pectoral fins extended as lifting hydrofoils to counter their weight in water. Their gas bladder is often reduced or absent. Typical speeds were observed from seven species and compared with the speeds expected from them to maintain hydrostatic equilibrium. The expected speeds were computed from a model I developed using data on the lifting area of extended pectoral fins and the weight of the fish in water.

Lifting areas of the pectoral fins were determined from photographs of dead fishes. Mass-length relations were determined and converted to weight in water from data on water density and fish density.

Typical observed speeds varied among species from 0.33 to 2.19 lengths/sec. Scombroids of the same fork length differed greatly in mass, density, and pectoral fin areas. Swimming speed required for maintaining hydrostatic equilibrium should be greater for fishes with greater mass, higher density, and smaller pectorals. Expected speeds were computed. They were highly correlated with observed speeds, $r = +0.89$. Thus, the model accurately predicted typical swimming speeds of scombroids, which suggests that variations in mass, density, and the lifting area of the pectoral fins, through the mechanism of maintaining hydrostatic equilibrium, can account for about 80% of the variation in typical swimming speeds. Expected speeds (centimeters per second) generated from the model either increased with fork length or reached a maximum and declined for larger fish. The latter pattern occurred if gas bladders were relatively larger in older fish or even absent in younger fish.

Scombroids with faster typical speeds have larger dark muscles and higher concentrations of blood hemoglobin than those with slower speeds. Differences in body shape were not closely related to differences in typical speeds.

Larger fishes should have more difficulty maintaining a speed which is sufficient for hydrostatic equilibrium without a gas bladder or large pectoral fins. The occurrence of gas bladders and long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes. Both were more common among larger species. Each species with a maximum mass ≥ 70 kg had a gas bladder while only 26% of those species ≤ 6 kg had a gas bladder. Further analyses suggested that a gas bladder and large pectorals may be increasingly more important for large species if they are to swim at energetically prudent speeds.

Scombroid fishes are negatively buoyant, pelagic, oceanic fishes. The scombroids include the mackerels, tunas, and bonitos. They swim continuously with pectoral fins extended. This behavior produces lift that balances their weight in water. Some attain large size. Xiphoids are the largest teleosts and powerful swimmers that share the pelagic environment with the scombroids.

General considerations of buoyancy mechanisms of negatively buoyant fishes are discussed by Aleev (1963) and Alexander (1967, 1968).

In regard to scombroids, Magnuson and Prescott (1966) observed that continuous swimming was apparently not entirely determined by a need for gill ventilation, as Pacific bonito,

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Sarda chiliensis, swam with their mouth closed as much as 40% of the time. Presumably the fish could have conserved energy by swimming more slowly with the mouth open more often. Minimum speed was also not regulated for food search (Magnuson, 1969); kawakawa, *Euthynnus affinis*, swam at the same speed day and night even though they were exclusively diurnal feeders. When deprived of food for several days, they swam slower and slower in absence of food stimuli. If typical speed had been regulated by feeding motivation, the fish would have been expected to swim faster—become more active—as motivation to feed increased.

Typical swimming speeds of *E. affinis* were well explained by the minimum speed required to produce sufficient lift on the pectoral fins to keep from sinking. Magnuson (1970) presented a model to predict minimum speed required of *E. affinis* to maintain hydrostatic equilibrium. Minimum speeds were estimated from the animal's weight in water and the lifting area, primarily of the pectoral fins.

Differences between the morphology and typical speeds of yellowfin tuna, *Thunnus albacares*, and *E. affinis* (Magnuson, 1966a) suggested that the variations in area of pectoral fins and volume of gas bladder might also be explained as various solutions for countering negative buoyancy. Many other specializations of scombroids related to swimming speed and activity may be adaptations to the speeds required for hydrostatic equilibrium rather than maximum, burst speeds (Magnuson, 1970).

In regard to xiphoids, a recent review on their functional morphology by Ovchinnikov (1970) did not consider the gas bladder or buoyancy mechanisms in discussions on the function of pectoral fins.

Purposes of the present paper are to (1) test whether the model mentioned above generally predicts typical swimming speeds of scombroid fishes, (2) consider the adaptive radiation in the morphology especially of the gas bladder and pectoral fins which together with swimming speed contribute to the mechanism by which scombroids maintain hydrostatic equilibrium, and (3) consider problems associated with large body size and maintenance of hydrostatic equilibrium among scombroid and xiphoid fishes.

SWIMMING SPEEDS

Typical swimming speeds were observed for five scombroid fishes in 7.2-m diameter swimming pools at Kewalo Basin, Honolulu, Hawaii, from underwater photographs of wahoo, *Acanthocybium solandri*, swimming at sea, and from previously published records on *Sa. chiliensis* (Magnuson and Prescott, 1966). Observed swimming speeds were determined or available for seven species of six different genera.

Methods for obtaining swimming speeds were described by Magnuson (1969). Fishes were observed for short periods at 1- to 4-hr intervals (0000-2400) during their first month in captivity. Observations were made for two consecutive 24-hr periods during which the fish were fed and not fed (Figure 1). On fed days they were fed to satiation with thawed smelt or shrimp once or twice usually at 0900 and 1600 hr. Data collected during the "day not fed" and the "night after not fed" were used for the estimates of the minimum typical swimming speed to compare with body morphology. These estimates were based on 19-212 min (median 68 min) of recorded speeds for each species. With the exception of 36-cm long bigeye tuna, *Thunnus obesus*, where only 1 fish was observed, measurements from 6 to 40 fish (median 12 fish) made up each estimate. Water temperatures were 23°-26°C and salinity 33‰.

Typical speeds of *Ac. solandri* were from 17 cinema sequences averaging 2.59 sec each. The films were taken from underwater viewing ports in the RV *Charles H. Gilbert* and an observation raft described in Nakamura (1972).

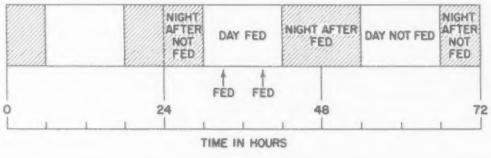

FIGURE 1.—Observation schedule for measurements of typical swimming speeds presented in Figure 2.

The observations that scombroid fishes swim continuously (Figure 2) would appear to be generalizable but the speeds, expressed either as body lengths per second (*l*/sec) or centimeters per second (cm/sec), differ considerably from one species to another or within species depending upon the size. Typical speeds ranged from 0.33 *l*/sec for *Ac. solandri* to 2.19 *l*/sec for the bullet mackerel, *Auxis rochei*. All species other than *Ac. solandri*, namely the skipjack tuna, *Katsuwonus pelamis*, *Sa. chiliensis*, *E. affinis*, *T. obesus*, *T. albacares*, and *Au. rochei*, had typical speeds greater than 1 *l*/sec. None of the species ever stopped swimming. The slowest speeds observed ranged from 0.12 *l*/sec for *Ac. solandri* to 1.97 *l*/sec for *E. affinis*. The typical speed of *T. obesus*, 36 cm FL (fork length), was 1.31 *l*/sec but the larger 55-cm *T. obesus* swam only 1.08 *l*/sec. Three length groups of the *K. pelamis* were also observed and their speeds differed among sizes.

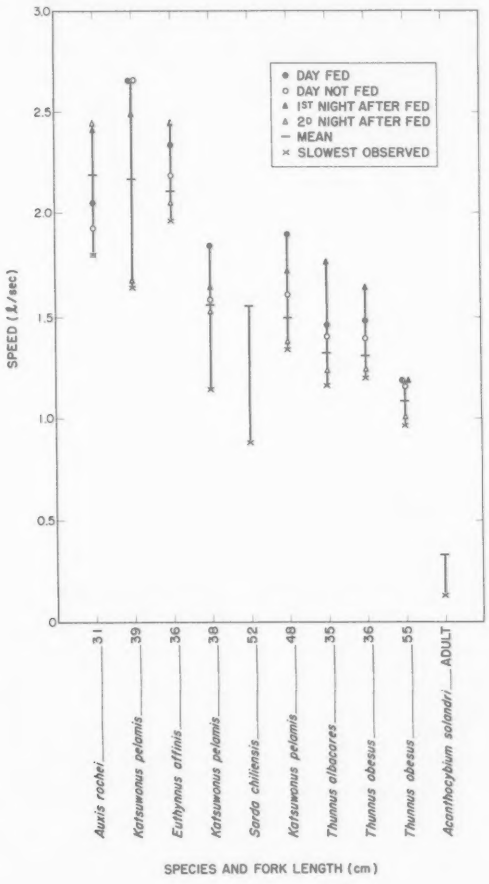

FIGURE 2.—Typical swimming speeds of seven scombroids.

SPEEDS REQUIRED FOR HYDROSTATIC EQUILIBRIUM

Variations in the typical swimming speeds among scombroids would result from differences in both the weight of the fish in water and the lifting area of the pectoral fins. Weight in water depends on mass and density of the fish. All specimens of chub mackerel, *Scomber japonicus*, and *Sarda chiliensis* used for morphometric and mass measurements were collected near Los Angeles, Calif. Specimens of all other species were collected in the central Pacific almost always near the Hawaiian Islands.

Variations in Weight

Not all scombroids have the same mass-length relationship (Figure 3). *K. pelamis* was heaviest and *Ac. solandri* lightest at a given length. For example, at a length of 75 cm, *Ac. solandri* has a mass less than 2 kg and *K. pelamis* greater than 9 kg. Other species were intermediate.

When submerged in water the fish displaces water which also has mass. If the gas bladder is large enough, the volume of water that a fish displaces may have the same mass as the fish. The weight of the fish in water, or conversely the lift required to keep the fish from sinking, is equal to the excess mass of the fish times the acceleration of gravity (Alexander, 1967; Magnuson, 1970). The excess mass of the fish is the difference between the mass of the fish and the mass of the water it displaces. It can be computed by multiplying the mass of the fish by $(1 - \frac{D_e}{D_f})$ where D_e is the density of the environment or seawater and D_f is the density of the fish. The

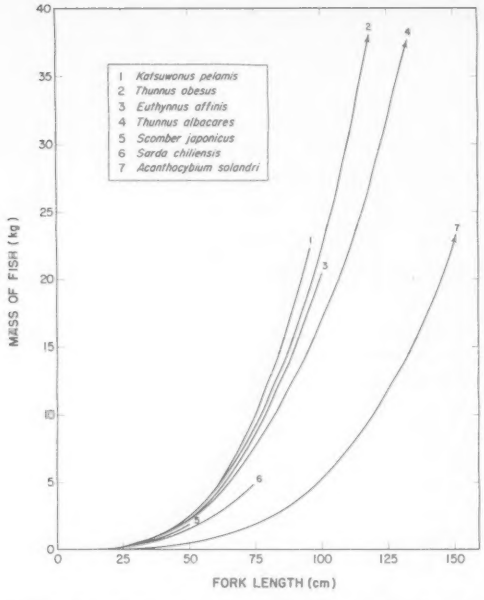

FIGURE 3.—Comparison of mass against length relationships among seven scombroid species. Information on regression equations in Table 4.

acceleration of gravity, g, is equal to approximately 980 cm/sec^2.

The influence of a gas bladder can be clearly seen by contrasting data for *K. pelamis* with *T. albacares*. Gas bladder volumes were determined with an x-ray method of Chang and Magnuson (1968) on fish immediately after they were killed. *K. pelamis* has no gas bladder but *T. albacares* has a gas bladder which grows allometrically, becoming progressively larger as the fish increases in mass (Figure 4a). *T. albacares*, 2 kg or less, has no gas in the bladder, but the gas bladder then grows rapidly until the fish is at least 8 kg. These differences in gas bladders of *K. pelamis* and *T. albacares* influence the density of the two species (Figure 4b). The density of *K. pelamis* remains approximately the same over the entire size range. However, once the gas bladder begins to grow in *T. albacares* the density of the fish becomes less, decreasing from approximately 1.09 g/ml for 2-kg fish to 1.05 g/ml for 10-kg fish. These differences in density have a corresponding influence on the lift required to keep the fish from sinking (Figure 4c). The lift required for *K. pelamis* increases in almost direct proportion to the increase of mass. But the lift required to keep *T. albacares* from sinking increases more slowly as the density of the fish becomes less. In fact, the lift required to keep *T. albacares* from sinking appears to approach asymptotically a maximum near 200×10^3 dynes.

Variations in the densities of various species and sizes can be examined in Table 1, where the mean densities of various species are given and the multipliers are computed to convert the mass of the fish to the lift required to keep them from sinking. All species with markedly lower densities, such as *Sc. japonicus*, *T. albacares*, *T. obesus*, and *Ac. solandri*, have gas bladders at some point in their life history. The more dense species, *Sa. chiliensis*, *Au. rochei*, *E. affinis*, and *K. pelamis*, have no gas bladder.

Lift to prevent the fish from sinking is 10 to 20 times greater for larger *K. pelamis*

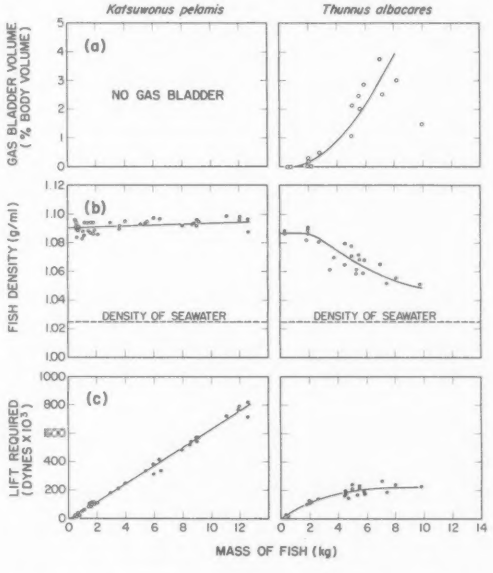

FIGURE 4.—Comparisons between *Katsuwonus pelamis* and *Thunnus albacares* of the relations between fish mass and (a) gas bladder volume, (b) fish density, and (c) lift required for hydrostatic equilibrium.

TABLE 1.—Densities (D_f) of eight scombroid species by size group and the multipliers to convert mass of fish (M_f in grams) to the lift (L in dynes) required for hydrostatic equilibrium. Multipliers[1] computed for seawater with densities of 1) 1.022 g/ml and 2) 1.025 g/ml. Measurements by methods described by Magnuson (1970).

Mass	*Scomber japonicus*	*Acanthocybium solandri*	*Sarda chiliensis*	*Auxis rochei*	*Euthynnus affinis*	*Katsuwonus pelamis*	*Thunnus albacares*	*Thunnus obesus*
0.00-1.99 kg:								
Number of fish	18		3	12	36	47	3	1
D_f (g/ml):								
Mean	1.054		1.075	1.086	1.087	1.090	1.086	1.066
SD	0.011		0.004	0.002	0.004	0.003	0.003	
Range	1.024		1.069	1.082	1.074	1.083	1.082	
	1.069		1.080	1.089	1.093	1.096	1.088	
Multiplier (1)	28.0		48.4	57.8	58.6	61.2	57.8	40.5
(2)	28.0		45.7	55.1	56.0	58.5	55.1	37.7
2.00-3.99 kg:								
Number of fish			10		23	4	4	17
D_f (g/ml):								
Mean			1.080		1.088	1.090	1.087	1.047
SD			0.006		0.009	0.003	0.004	0.010
Range			1.067		1.082	1.086	1.081	1.026
			1.086		1.094	1.094	1.090	1.064
Multiplier (1)			52.7		59.5	61.2	58.6	23.4
(2)			50.0		56.8	58.5	56.0	20.7
4.00-5.99 kg:								
Number of fish					3	4	12	
D_f (g/ml):								
Mean					1.091	1.094	1.068	
SD					0.004	0.001	0.007	
Range					1.086	1.093	1.059	
					1.095	1.095	1.080	
Multiplier (1)					62.3	64.6	42.2	
(2)					59.3	61.8	40.0	
6.00-7.99 kg:								
Number of fish						2	2	
D_f (g/ml):								
Mean						1.097	1.058	
SD						0.000	0.006	
Range						1.097	1.052	
						1.097	1.065	
Multiplier (1)						67.0	33.4	
(2)						64.4	30.6	
8.00-9.99 kg:								
Number of fish						6	2	
D_f (g/ml):								
Mean						1.094	1.054	
SD						0.001	0.002	
Range						1.093	1.051	
						1.096	1.056	
Multiplier (1)						64.6	29.8	
(2)						61.8	27.1	
≥ 10.00 kg:								
Number of fish		7				5		
D_f (g/ml):								
Mean		1.028				1.096		
SD		0.007				0.004		
Range		< 1.022				1.088		
		1.042				1.099		
Multiplier (1)		5.78				66.3		
(2)		2.94				63.5		
All sizes (without gas bladders only):								
Number of fish			13	12	62	68		
D_f (g/ml):								
Mean			1.078	1.086	1.087	1.091		
SD			0.006	0.002	0.004	0.004		
Range			1.067	1.082	1.074	1.083		
			1.086	1.089	1.095	1.099		
Multiplier (1)			51.0	57.8	58.6	62.0		
(2)			48.2	55.1	56.0	59.3		

[1] $[(1 - \frac{D_e}{D_f})980]$ where D_e is the density of environment.

(no gas bladder) than for *Ac. solandri*, which has a large gas bladder. These differences would also significantly influence the speed required to maintain hydrostatic equilibrium, and on this basis species without gas bladders are expected typically to swim faster than those with gas bladders.

Variations in the Lifting Area of Pectoral Fins

The lift produced by a hydrofoil is directly proportional to its lifting area, thus those species with a larger lifting surface should be capable of swimming at a slower speed, all other things being equal. The primary lifting surfaces of *E. affinis* are the pectoral fins (Magnuson, 1970), although other surfaces such as the caudal keel may counter some of the weight. The lifting area of the pectoral fins is the area of the extended pectoral fins as viewed from above plus the area of the body between the fins. It was determined for the various species from photographs of dead fish as described by Magnuson (1970).

Pectoral fins of scombroids are analogous to variable sweepback wings; they can be fully extended, swept back, or laid against the body (Magnuson, 1970). Species such as *E. affinis* and *K. pelamis* swam with the fins swept back about 40°, but the two species with the largest pectoral fins, *T. albacares* and *T. obesus*, swam with the fins swept back about 60° (Table 2). Sweepback angles measured from dead fish used for morphometric measurements were not as great as those from fish swimming in tanks. Measurements from dead fish were 7° and 14° for *E. affinis* and *K. pelamis* and 29° and 36° for *T. albacares* and *T. obesus*. Thus, some bias occurs in the estimation of the lifting area for swimming fish from the dead fish. This bias is probably slight because, although the actual area of the pectoral fin decreases rapidly as the fins are swept back, the total lifting area does not (Magnuson, 1970). Measurements of sweepback from other dead fishes used for morphometric measurements averaged 10° for *Sc. japonicus*, 24° for *Ac. solandri*, 16° for *Sa. chiliensis*, and 10° for *Au. rochei*.

Differences in pectoral fin lifting areas among scombroids are illustrated in diagrammatic dorsal views of seven species at the same length (Figure 5). Lifting areas differ markedly among species and among sizes for the same species (Figure 6). *T. obesus* has, among the species here, the largest lifting

TABLE 2.—Average sweepback of pectoral fins for swimming captive fishes. *n* equaled the number of fish. Λ was averaged for left and right fins.

Species	Day fed			Day not fed[1]			Fed and not fed combined		
	Λ (degrees)		*n*	Λ (degrees)		*n*	Λ (degrees)		*n*
	Mean	SD		Mean	SD		Mean	SD	
Euthynnus affinis	34	8.5	15	32	12	15	43	10	30
Katsuwonus pelamis	43	15	101	43	13	53	43	14	154
Thunnus albacares	61	3.1	11	55	3.7	3	60	4.0	14
Thunnus obesus	61	5.0	64	56	7.5	45	59	6.7	109

[1] Two days after fed for *E. affinis* and *T. albacares*; 1 day after fed for *K. pelamis* and *T. obesus*.

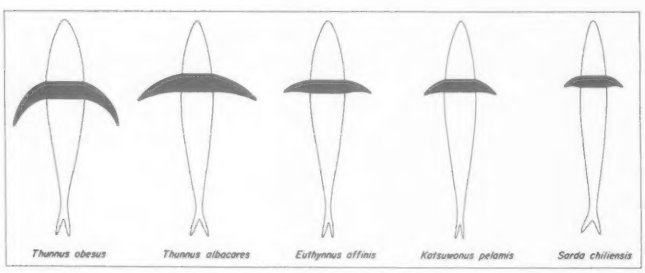

FIGURE 5.—Diagrammatic dorsal views of five scombroid species to dramatize the variation in the lifting areas of the pectoral fins for various species. Drawn from photographs of dead fish ca. 50 cm in fork length.

area at a given length, and *Ac. solandri* has the smallest. For example, at a fork length of 125 cm, *T. obesus* has a lifting area greater than 500 cm², whereas *Ac. solandri* has a lifting area near 150 cm² (Figure 6). These differences should have a marked effect on the minimum speed required to maintain hydrostatic equilibrium. Those with larger pectorals such as *T. albacares* and *T. obesus* should have a slower minimum speed than those with smaller pectorals.

Predicted Swimming Speed

The model used by Magnuson (1970) to predict the minimum speed required for hydrostatic equilibrium was

$$V_{100} = \left[\frac{L_t}{\rho/2\,(C_{L_f} A_{f_t} + C_{L_k} A_k)}\right]^{1/2}. \qquad (1)$$

All terms used here and elsewhere in this paper are listed below:

l = fork length (cm)
L_t = total weight of fish in water (dynes)
L_f = all lift produced by the total lifting area of the pectoral fins (dynes)
L_k = lift produced by keel (dynes)
A_{f_e} = area of pectoral fins
A_{f_t} = total lifting area of pectorals (cm²)
A_k = lifting area of keel (cm²)
C_{L_f} = coefficient of lift for the pectoral fins based on all lift produced by pectorals and on total lifting area of pectorals
C_{L_k} = coefficient of lift for the keel
V_{100} = speed of fish with pectorals continuously extended (cm/sec)
Λ = sweepback angle of pectoral fins (degrees)
D_e = ρ = density of water = 1.022 g/ml in Kewalo tanks, 1.025 g/ml at sea
D_f = density of fish (g/ml)
M_f = fish mass.

To test predictive value of this model for a number of species, computed speeds were compared with observed speeds. Typical swimming speeds were computed twice: first, assuming the keel provided significant lift, and second, assuming all the lift was provided by pectoral fins. Results from these computations and the data used to make them are presented in Table 3. Regressions in Table 4 were used to determine the mass of the fish and the area of the lifting surfaces for calculations of minimum hydrostatic speeds. The mass of the fish was converted to required lift by using the conversion factors from Table 1. Lift coefficients were from Table 7 of Magnuson (1970)—those determined for *E. affinis* on the basis of total lifting area of the pectorals.

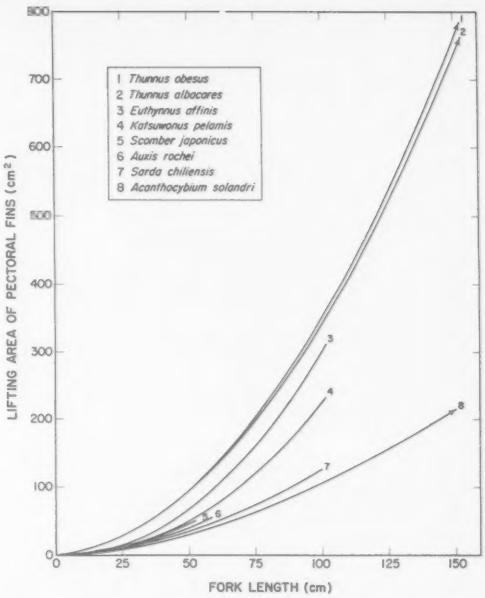

FIGURE 6.—Comparison of lifting area of pectoral fins against length relationships among eight scombroid species. Information on regression equation in Table 4.

Several comments should be made about the use of the lift coefficients from *E. affinis* for all species considered in the present text. The lift coefficient calculated on the basis of the total lifting area of pectorals represents lift on the pectorals, interference lift on the body owing to the pectorals, and the interference lift on the pectorals owing to the presence of the body. At best the coefficient is only a convenient but arbitrary standard frequently used in aerodynamic literature.

TABLE 3.—Computed speeds required for hydrostatic equilibrium and the morphometric data used to make the computations along with the typical swimming speeds observed for scombroids. Lift coefficients from Magnuson (1970). Masses, areas, and required lift from equations in Table 4 and fork length of captive fishes.

Species	l (cm)	(a) M_f (g)	(b) Multiplier to convert M_f to L_t	(a × b) L_t (dynes × 10^3)	A_K (cm^2)	(c) A_{Lf} (cm^2)	Surface loading of pectorals ($L_t \div A_{Lf}$) (dynes/cm^2)	Computed hydrostatic speeds (V_{100})[1] Without keel[2] (cm/sec)	(l/sec)	With keel[3] (cm/sec)	(l/sec)	Observed speed of fishes (cm/sec)	(l/sec)
Auxis rochei	31	498	57.8	28.8	[4]3.3	17.7	1,630	56	1.8	57	1.8	68	2.2
Katsuwonus pelamis	39	1,090	61.2	66.7	5.51	27.4	2,430	69	1.8	70	1.8	84	2.2
Euthynnus affinis	36	832	58.6	48.8	5.41	31.6	1,540	55	1.5	56	1.6	76	2.1
Katsuwonus pelamis	38	996	61.2	61.0	5.20	25.9	2,360	68	1.8	69	1.8	59	1.6
Sarda chiliensis	57	2,320	52.7	122.	11.8	45.9	2,660	72	1.3	71	1.2	88	1.5
Katsuwonus pelamis	48	2,180	61.2	133.	8.79	43.7	3,040	77	1.6	78	1.6	72	1.5
Thunnus albacares	35	858	57.8	49.6	6.11	47.0	1,060	45	1.3	47	1.4	46	1.3
Thunnus obesus	36	854	40.5	34.6	5.87	52.1	664	36	1.0	38	1.0	47	1.3
Thunnus obesus	55	3,290	23.4	77.0	15.8	116.	664	36	0.66	38	0.68	60	1.1
Acanthocybium solandri	125	[5]12,400	[6]5.78	71.7	51.6	163.	440	29	0.23	28	0.22	[7]41	0.33

[1] With equation 1. [2] $C_{L_K} = 0, C_{L_f} = 1$. [3] $C_{L_K} = 0.9, C_{L_f} = 0.8$.
[4] Estimated by comparing data with *K. pelamis* and then taking from *K. pelamis* regression.
[5] Estimated from length-weight relation given by Iversen and Yoshida (1957).
[6] From Table 1, $D_e = 1.022$ g/ml.
[7] Speed (cm/sec) = speed (*l*/sec) × length (cm) = 0.33 × 125 = 41.

Lift coefficients vary with sweepback, angle of attack, aspect ratio, the ratio of fin span to body width, and taper ratio (Lawrence and Flax, 1954). The differences in these parameters among species or within species were not evaluated, but comparisons made below between observed and calculated speeds suggest that the assumption about a constant lift coefficient based on total lifting area was not too bad. The coefficients used here should be more accurate for scombroids with short pectorals because *E. affinis* has short pectorals. The span of the pectorals, tip to tip, for *E. affinis* is about 2.4 times the body width.

Correlation coefficients (Table 5) were computed to discover how closely the observed swimming speeds were associated with fork lengths of the fish, the mass of the fish, the required lift to keep the fish from sinking, the lifting area of pectoral fins, the surface loading of pectoral fins, and the predicted swimming speed. Relations between observed speed and fork length, mass of fish, required lift, and lifting area of the pectoral fins were all nonsignificant statistically. But when required lift and the lifting area were considered jointly as surface loading of the pectorals, the correlation was significant ($P < 0.005$). Surface loading is the weight carried per unit area of lifting surface. Predicted speeds were also highly correlated with observed speeds (Table 5, Figure 7). The highest correlation, +0.89, between observed and predicted speeds in body lengths per second suggested that the hydrostatic equilibrium requirement of continuous swimming accounts for approximately 80% of the variation in observed swimming speeds. The model predicts typical swimming speeds of scombroids well and suggests that the variations in mass, density, and the lifting area of the pectoral fins can account for almost all variations in observed swimming speeds among scombroids.

Observed speeds averaged 9.8 cm/sec or 0.2 *l*/sec faster than computed speeds. The computation of V_{100} assumed that the pectorals were continuously extended but this was not always the case. Thus, the fact that observed speeds were greater than V_{100} is not surprising. *E. affinis*, for example, had the pec-

TABLE 4.—Regression equations ($\log y = \log a + b \log l$) with relevant data and 95% confidence intervals used to compute fish mass (M_f), area of pectoral fins (A_{f_e}), lifting area of pectoral fins (A_{f_t}), and keel area (A_k) for nine species of scombroid fishes. Measurements made by methods described in Magnuson (1970).

y	Species	n	Range in l (cm)	log l	log y	log a	a	b	S_b	SE est.	Confidence limit on b	Confid. limit on $\overline{\log y}$ $\overline{\log l}$
M_f	*Sc. japonicus*	20	26.9- 41.4	1.5434	2.7630	—2.4353	0.00367	3.37	0.1458	0.0345	±0.31	±0.0725
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	3.3647	-1.4100	0.0389	2.72	0.1770	0.0284	±0.39	±0.0625
	Au. rochei	11	33.9- 40.4	1.5546	2.9038	-2.3143	0.00485	3.36	0.4557	0.0290		
	E. affinis	63	31.6- 67.8	1.6251	3.1383	-1.9666	0.0108	3.14	0.0388	0.0632	±0.08	±0.1265
	K. pelamis	68	24.1- 82.9	1.6395	3.1977	-2.3098	0.00490	3.36	0.0180	0.0212	±0.04	±0.0424
	T. albacares	52	28.4-106.9	1.7859	3.6236	-1.4828	0.0329	2.86	0.0420	0.0325	±0.08	±0.0653
	T. obesus	26	36.3-150.5	1.8421	3.8440	-2.0173	0.00961	3.18	0.0868	0.1606	±0.18	±0.3315
A_{f_e}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.0005	-2.1543	0.00701	2.05	0.1864	0.0426	±0.39	±0.0881
	Ac. solandri	7	122.8-148.8	2.1112	1.9565	-2.1931	0.00641	1.97	0.7864	0.0551	±2.02	±0.1417
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.3020	-2.2358	0.00581	2.02	0.4993	0.0800	±1.10	±0.1761
	Au. rochei	11	31.9- 40.4	1.5499	1.0380	-2.0348	0.00923	1.98	0.7455	0.0586	±1.69	±0.1326
	E. affinis	37	33.7- 64.3	1.6440	1.3759	-2.3010	0.00500	2.24	0.0940	0.0475	±0.19	±0.0964
	K. pelamis	33	24.3- 82.9	1.7271	1.3722	-2.3840	0.00413	2.17	0.0562	0.0477	±0.11	±0.0974
	T. albacares	32	28.4-148.8	1.7920	1.9453	-1.2351	0.0582	1.78	0.0631	0.0602	±0.13	±0.1229
	T. obesus	25	46.1-150.5	1.8496	2.0613	-1.0477	0.0896	1.68	0.0445	0.0828	±0.09	±0.1713
A_{f_t}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.3394	-1.7012	0.0199	1.97	0.2520	0.0576	±0.65	±0.1481
	Ac. solandri	7	122.8-148.8	2.1112	2.2192	-1.5031	0.0314	1.76	0.5700	0.0399	±1.25	±0.0878
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.6472	-1.4634	0.0344	1.78	0.3892	0.0613	±0.86	±0.1350
	Au. rochei	10	31.9- 40.4	1.5505	1.3546	-1.2418	0.0573	1.67	0.7115	0.0557	±1.64	±0.1284
	E. affinis	37	33.7- 64.3	1.6440	1.6920	-2.0182	0.00959	2.26	0.0855	0.0432	±0.17	±0.0877
	K. pelamis	33	24.3- 82.9	1.7271	1.7402	-2.1255	0.00749	2.24	0.0545	0.0462	±0.11	±0.0943
	T. albacares	32	28.4-136.0	1.7920	2.1402	-1.2154	0.0609	1.87	0.0478	0.0456	±0.10	±0.0931
	T. obesus	25	46.1-150.5	1.8496	2.2599	-1.2090	0.0618	1.88	0.0391	0.0366	±0.08	±0.0757
A_k	*Sc. japonicus*	—	—	—	—	—	—	—	—	—	—	—
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.0761	-1.2104	0.0616	1.30	0.4784	0.0766	±1.05	±0.1687
	Au. rochei	—	—	—	—	—	—	—	—	—	—	—
	E. affinis	41	33.7- 67.8	1.6479	0.9548	-3.0017	0.000996	2.40	0.1501	0.2477	±0.30	±0.5011
	K. pelamis	34	24.3- 82.9	1.7128	1.0154	-2.8386	0.00145	2.25	0.0761	0.1308	±0.16	±0.2667
	T. albacares	36	34.0-136.0	1.8005	1.3687	-2.7033	0.00198	2.26	0.0986	0.1786	±0.20	±0.3624
	T. obesus	25	46.1-150.5	1.8496	1.4489	-2.8729	0.00134	2.34	0.1284	0.2387	±0.27	±0.4940

TABLE 5.—Correlations between observed speeds of scombroids and the fork length, mass, required lift for hydrostatic equilibrium, surface loading, and computed speeds with and without the keel included in the calculation.

Correlates		r_{xy}	$P(n = 10)$
y	x		
V_{obs} (cm/sec)	Fork length (l) (cm)	-0.37	N.S.
V_{obs} (cm/sec)	Mass of fish (M_f) (g)	+0.44	N.S.
V_{obs} (cm/sec)	Required lift (L_t) (dynes)	+0.44	N.S.
V_{obs} (cm/sec)	Lifting area of pectorals (A_{f_t}) (cm^2)	-0.54	N.S.
V_{obs} (cm/sec)	Surface loading of pectorals (dynes/cm^2)	+0.77	<0.005
V_{obs} (cm/sec)	V_{100} without keel (cm/sec)	+0.79	<0.005
V_{obs} (cm/sec)	V_{100} with keel (cm/sec)	+0.78	<0.005
V_{obs} (l/sec)	V_{100} without keel (l/sec)	+0.89	<0.0005

torals extended only about 75% of the time at typical speeds. The percent of extension of the pectorals varied greatly from species to species. The species with the longest pectorals, *T. obesus* and *T. albacares*, almost never appressed their pectoral fins while swimming at typical speeds.

Typical speeds of each species over its length range (Figure 8) were computed from equation 1 using values for M_f, A_{f_l} from Table 4, and values of D_e from Table 1, ρ was set at 1.025 g/ml. Since the inclusion of lift from the keel had little effect on computed speeds (Table 3), the computations were made on the basis that all lift came from the pectorals.

The three species with the fastest predicted swimming speeds—*K. pelamis*, *Sa. chiliensis*, and *E. affinis*—have no gas bladder (Figure 8), while species with the lowest predicted speeds—*T. albacares*, *T. obesus*, *Sa. japonicus*, and *Ac. solandri*—have gas bladders. *Ac. solandri*, the species with the lowest predicted speed, has the largest gas bladder and the lowest density.

Among the three species without gas bladders, *K. pelamis* is the heaviest for its length and has the fastest minimum speed. The predicted speeds of *Sa. chiliensis* and *E. affinis* are quite similar, even though *E. affinis* is considerably heavier at a given length than

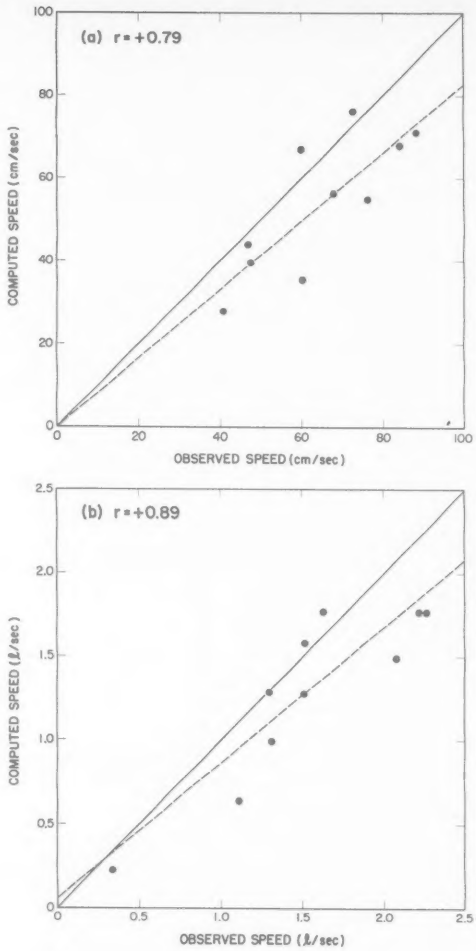

FIGURE 7.—Correlation between observed swimming speeds of scombroids and the computed minimum speed for hydrostatic equilibrium (a) in cm/sec, and (b) in body lengths/sec. Data from Table 3. Solid line shows expectation for perfect agreement and dashed line is the linear regression of expected speed on observed speed. Correlation coefficients, r, are given on graph.

Sa. chiliensis (Figure 3). This difference results from the difference in the lifting area of pectoral fins (Figure 6). *E. affinis* has lifting areas twice the size of *Sa. chiliensis* at a given length. Interestingly, the minimum speeds predicted for *K. pelamis* were almost identical to the speeds predicted by Shuleikin

(1966) as most efficient for migration by aquatic organisms.

Among the species with gas bladders, *T. albacares* and *T. obesus* have the largest pectorals, but *Ac. solandri* with small pectorals swims the slowest. The difference appears to be primarily from differences in gas bladder volume and resulting density. The large gas bladder and low density of *Ac. solandri* more than compensate for small pectoral fins.

At larger sizes all species swim slower in body lengths per second (Figure 8b), but owing to the allometric growth of the gas bladder, both large *T. albacares* and *T. obesus* can swim at slower speeds even in absolute units (centimeters per second). Their weights in water increase more slowly than their lifting areas after the fish attain approximately 50 cm FL.

A word of warning about Figure 8 is that the predicted speeds are extrapolated outside of the range for which morphometric and body density data were available. In addition, the density data for *Ac. solandri* was based only on animals 125 cm long. Likewise, the density data on *T. obesus* was limited.

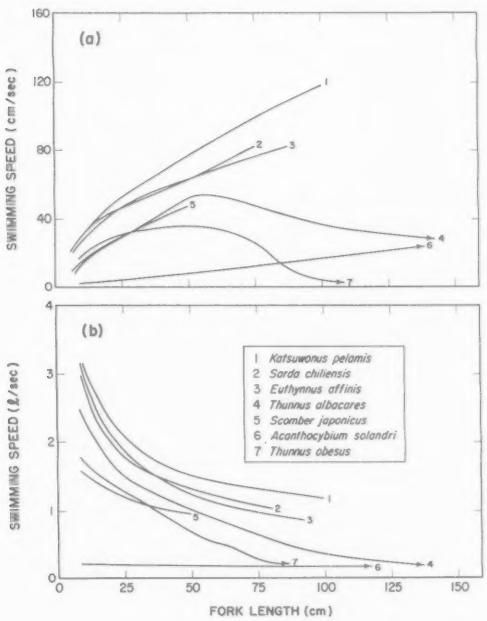

FIGURE 8.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec. Estimates from equation 1 and data in Table 4. See text for explanation.

OTHER FEATURES ASSOCIATED WITH BASAL SPEED

Scombroid fishes have many adaptations for efficient continued movement through the water. They have a high hemoglobin level (Klawe, Barrett, and Klawe, 1963), a large dark muscle (Kishinouye, 1923) for continuous locomotion (Rayner and Keenan, 1967), and a streamlined shape (Walters, 1962; Aleev, 1963; Alexander, 1967). The following analyses were to determine whether these adaptations were strongly associated with the basal or typical swimming speed. If differences in these characteristics varied closely with differences in typical speed, then I would argue that these adaptations were primarily selected for continuous slow swimming rather than maximum, burst speeds. Data on the burst or maximum speeds of these species are limited but do not indicate a strong association with typical speed. The burst speeds of 6-21 *l*/sec for *T. albacares* and 12-19 *l*/sec for *Ac. solandri* measured by Walters and Fierstine (1964) with a piscatometer at sea were approximately the same even though typical speed observed for *Ac. solandri* was less than one-fourth those of *T. albacares* (Table 3). Maximum speeds of four species measured photographically at sea or in shoreside tanks differ from species to species but not in relation to the typical speeds (Table 6).

TABLE 6.—Comparison of typical and maximum speeds observed from four scombroids.

Species	Speed (*l*/sec)		Source for maximum speeds
	Typical (Table 3)	Maximum	
Thunnus albacares	1.3	10	Yuen (1966)
Sarda chiliensis	1.5	6.5	Magnuson and Prescott (1966)
Katsuwonus pelamis	1.5 1.6 2.2	14.4	Yuen (1966)
Euthynnus affinis	2.1	12.5	Walters (1966)

Dark muscle size was determined from dissections of fresh material—the difference in the coloration of the dark muscle and the rest of the muscle block was sufficiently visible that the entire dark muscle could be removed and weighed. Its size was expressed as a percentage of fish mass. Body shape was determined from dorsal and lateral photographs of fresh dead fish. The maximum body height (H) and maximum body width (W) as a percent of fork length were averaged to represent the maximum thickness ($\frac{H + W}{2}$) of the body. The position of maximum thickness along the length of the fish was expressed as percent of fork length. It was determined by averaging the measurements from both dorsal and lateral views. Usually the position of maximum height for a species was 1 to 3% (of fork length) more posterior than the position of maximum width.

Data on dark muscle, blood hemoglobin, maximum body thickness, and the longitudinal position of maximum body thickness are presented for seven scombroid species in order of decreasing typical swimming speeds in Table 7. The size of the dark muscle (Table 7) ranged from 1.8% of the body mass for *Ac. solandri*, 125 cm long, to 10.3% of body mass for *Au. rochei*, 31 cm long. Within single species, the relative size of the dark muscle is smaller for larger animals. For example, *T. obesus* approximately 55 cm long have a dark muscle 7.7% of the body mass, whereas those 125 cm long have a red muscle of 4% of the body mass. I observed the same trend but with different magnitudes for other species for which a wide range of lengths were examined. Blood hemoglobin ranged from 10.4 g/100 ml of blood for *Ac. solandri* to 19.2 g/100 ml for *Au. rochei* (Table 7). This range includes values comparable to mammals—man for example has ca. 15 g/100 ml.

Typical speeds were positively correlated (Figure 9) with dark muscle size ($r = +0.86$, $n = 9$, $P < 0.005$) and with blood hemoglobin ($r = +0.83$, $n = 9$, $P < 0.005$). Approximately 70% of the variation in both dark muscle size and hemoglobin concentration are associated with variation in typical speeds. The size of the dark muscle and the concentration of hemo-

TABLE 7.—Relative size of dark muscle, blood hemoglobin concentration, and body morphology of various scombroids for comparison with the typical swimming speeds. Dark muscle and body morphology from present study. Fish ordered by decreasing swimming speeds (l/sec).

			Dark muscle			Hemoglobin		Body morphology						
Species	Fork[1] length (cm)	Observed speed (l/sec)	(% M_f)	95% confidence interval on mean	n	(g/100 ml)	Source	Fork[2] length (cm)	n	H Maximum body height (% l)	W Maximum body width (% l)	$(H + W) \div 2$ Maximum thickness (% l)	Distance from snout to position of maximum thickness (% l)
Au. rochei	31	2.19	10.3	±0.4	7	19.2	Barrett and Williams (1965)	32- 37	10	24.3	17.4	20.8	40.2
K. pelamis	39	2.17	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
E. affinis	36	2.11	8.1	±0.5	22	—	—	37- 43	7	27.2	18.0	22.6	40.4
K. pelamis	38	1.55	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
Su. chiliensis	57	1.54	6.2	±0.4	4	12.9	Barrett and Williams (1965)	45- 65	12	21.8	15.1	18.4	39.5
K. pelamis	48	1.49	7.5	±0.3	18	16.7	Barrett and Connor (1962)	44- 57	12	26.3	18.6	22.4	42.0
T. albacares	35	1.31	7.4	—	2	14.3	Barrett and Connor (1962)	28- 45	6	27.8	16.8	22.3	41.2
T. obesus	36	1.31	—	—	—	15.6	Barrett and Williams (1965)	46- 48	3	28.6	17.9	23.2	35.5
T. obesus	55	1.08	7.7	±0.6	13	15.6	Barrett and Williams (1965)	50- 60	13	28.7	18.5	23.6	37.5
Ac. solandri	125	0.33	1.8	±0.5	6	10.4	Barrett and Williams (1965)	123-130	6	14.6	10.4	12.5	37.3

[1] Lengths of fish observed for swimming speed. Dark muscle data for fish of approximately same lengths.
[2] Lengths for body morphology.

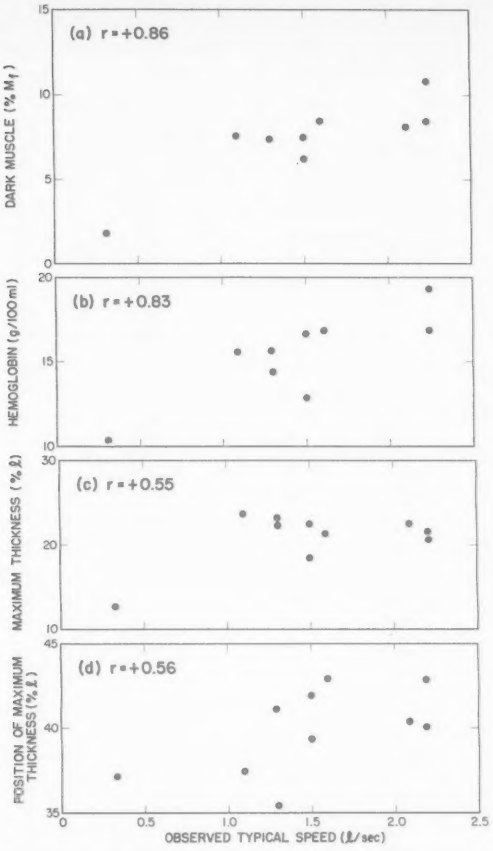

FIGURE 9.—Relation between observed swimming speeds and (a) the relative size of the dark muscle and (b) the concentration of blood hemoglobin, (c) maximum thickness of body, and (d) the position of maximum thickness along the length of the fish. Data from Table 7. Correlation coefficients, r, are given on graph.

globin are also highly correlated ($r = +0.82$, $n = 8$, $P < 0.005$). As expected, the dark muscle used for continuous slow speed is larger for species with faster typical swimming speeds. However, concentrations of blood hemoglobin also appear to be keyed to typical speeds and routine metabolism. Differences in need to transport oxygen sufficient for burst speeds apparently influenced hemoglobin levels little. Perhaps this is so because an oxygen debt can be temporarily incurred for burst activity.

Typical speeds in body lengths per second (Figure 9c, d) were also correlated with maximum thickness of the body ($r = +0.55$, $n = 10$, $P < 0.05$) and with the position of maximum thickness ($r = +0.56$, $n = 10$, $P < 0.05$). If speed is given in centimeters per second, the correlation $+0.21$ and $+0.49$ with maximum thickness and the position of maximum thickness are not statistically significant at $P < 0.05$.

Maximum thickness of the body ranged from 12.5 to 23.6% of fork length but only *Ac. solandri* had a value less than 18% (Table 7). Only 30% of the variability in thickness is associated with typical speeds. Thus, these variations do not appear to be closely related to differences in typical speeds (Figure 9c) with the exception that the species with the lowest typical speed, *Ac. solandri*, also had a low thickness ratio that would not be expected to minimize drag. Minimum drag should result from thickness ratios near 22% (Alexander, 1967). Differences among *Auxis*, *Katsuwonus*, *Sarda*, and *Thunnus* vary over a narrow range near 22% in a manner not related to typical swimming speeds.

Scombroids with faster typical speeds tend to have the thickest part of their body more posteriad (Figure 9d). Only 30% of this variation is associated with basal speed, but the trend is sensible in that the more laminar flow profiles should occur in the faster fishes.

In conclusion, all four characteristics, size of dark muscle, hemoglobin concentration, body thickness, and the position of the thickest part of the body are statistically related in a sensible manner to the variations in slow typical speeds of scombroids. The relations are poorer for the two characteristics involved in reducing drag, apparently because these features are more important at burst speeds than at typical speeds.

PROBLEMS ASSOCIATED WITH LARGE SIZE

Among the scombroid and xiphoid fishes, there is a great diversity in maximum body size, areas of pectoral fins, and the presence or size of the gas bladder. Data on these

TABLE 8.—Published data for scombroid and xiphoid fishes on maximum mass, the presence or absence of a gas bladder, and the relative length of pectoral fins. Species are ordered from smallest to largest known mass. Where only the length was known, mass was estimated from Figure 3 from a similarly shaped species.

Species	Maximum size			Gas bladder		Pectoral fins	
	Mass	Fork length	Source[1]	Present	Source[1]	Short (<20% FL) Long (≥20% FL)	Source[1]
	kg	*cm*					
Rastrelliger faughni	—	(20)	24	Yes	24	Short	24
Rastrelliger brachysoma	—	(22)	19	Yes	24	Short	19
Rastrelliger kanagurta	—	(28)	19	Yes	24	Short	19
Cybiosarda elegans	1	—	6	No	10	Short	9
Scomberomorus multiradiatus	—	—	—	—	—	Short	10
Scomber japonicus	—	(35)	3	Yes	24	Short	9
Scomber australasicus	—	(45)	1	Yes	24	Short	24
Scomberomorus queenslandicus	2	(75)	6	—	—	Short	10
Scomberomorus sierra	2	(59)	7	—	—	Short	10
Scomberomorus koreanus	—	(60)	10	—	—	Short	10
Scomberomorus sinensis	—	(65)	10	—	—	Short	10
Scomberomorus guttatus	—	(82)	6	No	9	Short	9
Auxis rochei	—	(60)	6	No	9	Short	8
Scomberomorus concolor	—	(68)	10	No	9	Short	9
Sarda orientalis	3	—	20	No	13	Short	13
Scomber scombrus	3	—	3	No	24	Short	9
Auxis thazard	4	—	15	No	9	Short	41
Scomberomorus tritor	4	(98)	31	No	9	Short	9
Scomberomorus maculatus	5	—	2	No	9	Short	9
Euthynnus lineatus	5	—	5	No	12	Short	12
Sarda sarda	5	—	4	No	21	Short	9
Scomberomorus semifasciatus	—	(100)	25	No	9	Short	25
Scomberomorus niphonius	—	(101)	25	No	9	Short	25
Sarda chiliensis	—	(72)	16	No	12	Short	9
Scomberomorus lineolatus	6	—	18	No	40	Short	40
Grammatorcynus bicarinatus	11	—	36	Yes	36	Short	36
Orcynopsis unicolor	13	—	32	No	32	Short	9
Allothunnus fallai	14	—	6	No	35	Short	6
Thunnus atlanticus	16	—	17	Yes	11	Long	11
Scomberomorus regalis	16	—	3	No	9	Short	9
Euthynnus affinis	—	(100)	6	No	21	Both	41
Katsuwonus pelamis	22	—	6	No	39	Short	14
Euthynnus alleteratus	—	(122)	23	No	12	Short	12
Thunnus tonggol	27	—	6	No (rudimentary)	11	Both	11
Scomberomorus cavalla	37	—	4	No	10	Short	25
Thunnus maccoyii	—	(145)	11	Yes	11	Long	11
Thunnus alalunga	44	—	6	Yes	11	Long	11
Gasterochisma melampus	—	(165)	6	Yes	9	Short	22
Scomberomorus commerson	59	—	29	No	10	Short	25
Acanthocybium solandri	63	—	6	Yes	9	Short	9
Gymnosarda unicolor	80	—	21	Yes	21	Both	37
Tetrapterus pfluegeri	90	—	33	Yes	28	Both	33
Tetrapterus angustirostris	90	—	33	Yes	28	Short	34
Tetrapterus belone	90	—	33	Yes	33	Short	33
Istiophorus albicans	90	—	33	Yes	28	Short	33
Tetrapterus albidus	90	—	33	Yes	28	Both	33
Thunnus albacares	135	—	6	Yes	11	Long	11
Istiophorus platypterus	150	—	30	Yes	28	Short	27
Tetrapterus audax	180	—	33	Yes	28	Both	34
Thunnus obesus	198	—	6	Yes	11	Long	11
Xiphias gladius	536	—	27	Yes	26	Short	27
Makaira mazara (Jordan and Snyder)	—	(430)	27	—	—	Both	27
Makaira indica	700	—	30	Yes	28	Long	27
Thunnus thynnus	730	—	38	Yes	11	Both	11
Makaira nigricans	900	—	33	Yes	28	Both	34

[1] Abe and Takashima (1959).
[2] Beardsley and Richards (1970).
[3] Bigelow and Schroeder (1953).
[4] Breder (1948).
[5] Calkins and Klawe (1963).
[6] Collette and Gibbs (1963).
[7] Collette, Talbot, and Rosenblatt (1963).
[8] Fitch and Roedel (1963).
[9] Fraser-Brunner (1950).
[10] Gibbs and Collette (pers. comm.).
[11] Gibbs and Collette (1966).
[12] Godsil (1954).
[13] Godsil (1955).
[14] Godsil and Byers (1944).
[15] Gosline and Brock (1960).
[16] Hildebrand (1946).
[17] Idyll and de Sylva (1963).
[18] Jones and Silas (1962a).
[19] Jones and Silas (1962b).
[20] Kikawa (1963).
[21] Kishinouye (1923).
[22] Lahille (1905).
[23] Marchal (1963).
[24] Matsui (1967).
[25] Munro (1943).
[26] Nakamura et al. (1951).
[27] Nakamura, Iwai, and Matsubara (1968).
[28] Norman and Fraser (1948).
[29] Ogilby (1954).
[30] Osipov, Kizevetter and Zhuravlev (1964).
[31] Postel (1955).
[32] Postel (1956).
[33] Robins and de Sylva (1963).
[34] Royce (1957).
[35] Serventy (1948).
[36] Silas (1963a).
[37] Silas (1963b).
[38] Tiews (1963).
[39] Waldron (1963).
[40] Williams (1960).
[41] Williams (1963).

characters were surveyed from the literature and are presented in Table 8. To determine whether the hydrostatic requirements of swimming have had some influence on or interact with the maximum size, the occurrence of gas bladders and the occurrence of long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes (Table 9). The distinction between short and long fins was arbitrarily set at a pectoral length of 20% or more of body length at any point in the life history.

Larger species apparently require a gas bladder but smaller species do not. All of the 14 species $\geq$ 70 kg had gas bladders but only 26% of 19 species $\leq$ 6 kg had gas bladders (Table 9). Medium size fish, 7-69 kg, were intermediate. The largest species without a gas bladder was *Scomberomorus commerson* at 59 kg (Table 8). Apparently the presence of a gas bladder is obligatory for those species greater than 60 kg. The gas bladder overcomes some weight in water, reduces minimum required speeds, and results in a design that could reduce energy expenditures for the larger species.

The larger fishes also tend to have relatively longer pectoral fins. Of the 15 species $\geq$ 70 kg, 67% have long pectorals at some stage in their life history but none of the 25 species $\leq$ 6 kg ever have long pectorals (Table 9). Medium size fish, 7-69 kg, were intermediate.

The two adaptations that make slower speeds possible, large pectorals and a gas bladder, have some tendency to occur together. Of 24 species without a gas bladder, 92% (22 species) have short pectoral fins and of 25 species with a gas bladder only 48% (12 species) have short pectoral fins (Table 8). Apparently small species require neither large pectorals nor a gas bladder to have a required swimming speed slow enough to maintain. For these species, in most cases, the advantages of not having a gas bladder or the drag associated with large pectoral fins have overweighed the advantage of a slow required speed in the course of evolutionary history. Apparently large species have achieved speeds slow enough for a consistent overall design by the joint effects of pectorals and the presence of a gas bladder. For these species if the gas bladder were large enough, large pectorals were not necessary; but if the gas bladder were not large enough, selection occurred for large pectorals.

Thus large species have a gas bladder and may or may not have long pectoral fins, while small species may or may not have a gas bladder and in neither case have long pectorals. In addition, large xiphoids with the large gas bladder may be able to use the pectoral for functions other than lift production. For example, the reduction of pelvic fins among xiphoids means that the pectorals must also produce any downward forces often ascribed to the pelvics.

The joint influences of maximum mass, body density, and lifting areas on minimum possible speeds give some perspective to the problem of large size (Figure 10). Surfaces of minimum swimming speeds were calculated for hypothetical 1-, 10-, and 100-kg scombroids with a lift coefficient of 1.0 for the pectoral fins. The keel was assumed to produce no lift. As expected, the smaller the gas bladder, that is, the greater $(D_f - D_e)$, the faster the fish must swim to maintain hydrostatic equilibrium. Also, the smaller the pectoral fins (A_{f_l}), the faster the fish must swim.

For small scombroids of 1 kg, changes in the density have little influence on required speed. And once the pectoral fins reach at least 50 cm^2, further increases in area have little influence on required speed. A 1-kg scombroid would be about 40 cm long. Fish this long

TABLE 9.—Occurrence of a gas bladder and the occurrence of long pectoral fins among scombroid and xiphoid fishes with different maximum masses. (A summary of Table 8.)

Item	Maximum mass (kg)						
	≤6		7-69		70-900		Total
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*
Gas bladder:							
Present	5	26	6	40	14	100	25
Absent	14	74	9	60	0	0	23
Total	19	100	15	100	14	100	48
Pectoral fins:							
Long	0	0	5	33	10	67	15
Short	25	100	10	67	5	33	40
Total	25	100	15	100	15	100	55

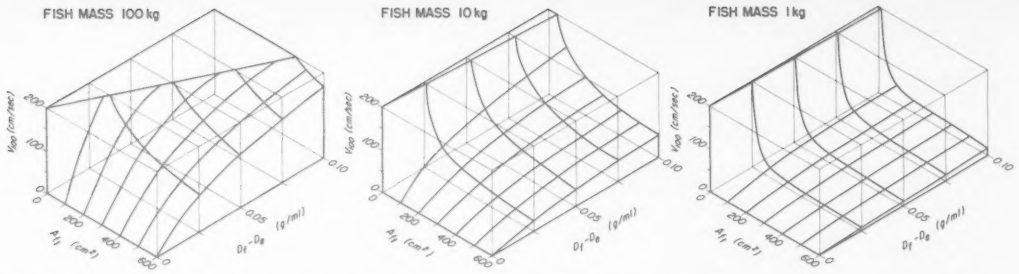

FIGURE 10.—Surfaces of minimum speeds required for hydrostatic equilibrium computed with different values of A_{f_t} and $(D_f - D_e)$ for hypothetical scombroids with a mass of 1, 10, or 100 kg. Speeds were computed from equation 1 with $\bar{C}_{L_f}$ set at 1.0 and D_e or ρ set at 1.025 g/ml.

should be able to maintain speeds near 100 cm/sec according to data from nonscombroids summarized in Figure 18 of Magnuson (1970). If there were some disadvantage to having a gas bladder, the loss of the bladder would not impose impossible levels of activity. Thus, the absence of a gas bladder and the occurrence of small pectorals among some small scombroids are consistent with the expectations of Figure 10 for 1-kg fish.

If hypothetical 10-kg and then 100-kg scombroids are considered (Figure 10), the presence of a gas bladder can be seen to be increasingly important to retain low levels of swimming activity. Required speed decreases rapidly with increasing pectoral size up to about 100 cm² for 10-kg fish and up to 200 cm² for 100-kg fish compared to 50 cm² for 1-kg fish. For a 100-kg fish and $(D_f - D_e) = 0.025$, as lifting areas increase from 200 to 700 cm², required speed declines to about 100 cm/sec. This constitutes a significant reduction in speed and helps explain why 100-kg *Thunnus* have pectoral lifting areas as great as 700 cm². Large scombroids could reduce energy expenditures with larger than expected pectoral fins.

Computed minimum speeds were slower than 40 cm/sec for a 100-kg *Thunnus* (Figure 8). If its pectoral fins were as small as those of *K. pelamis*, it would have to swim at least 90 cm/sec; and if it also had no gas bladder, its minimum speed would have to be 160 cm/sec.

Adaptations that serve to make low activity possible for large scombroids and xiphoids may reduce required speed well below the endurance speed or even below the most physiologically efficient speed for a species to migrate. No data on maximum endurance speeds are available for fish this large, but endurance speeds of sockeye salmon, *Oncorhynchus nerka*, in centimeters per second, increases as length increases (Brett, 1965). The relationship, speed $= 19\ l^{0.5}$, was determined from *O. nerka*, 8 to 54 cm FL, over periods only as long as 1 hr. Another data set (Hunter, 1971) for the jack mackerel, *Trachurus symmetricus*, is similar but based on shorter fish, 9-18 cm long, for longer periods, 6 hr. The relation was speed $= 22\ l^{0.6}$. Extrapolation of these relationships from a salmonid, 50 cm long, or a carangid, 18 cm long, to scombroids, about 80 and 180 cm long, seems a bit unrealistic, but if done indicates that the required speeds, even for a large hypothetical fish with short pectoral and no gas bladder, are considerably below the extrapolated endurance speeds. And a 100-cm *T. albacares* with its gas bladder and large pectorals swims at speeds less than one-sixth the extrapolated endurance speeds of a salmonid and less than one-fourth the speeds predicted by Shuleikin (1966) as most efficient for migration. Shuleikin's theoretical model was based on the speed at which the fish expended the least energy to overcome internal friction of muscles and external friction from movement through water.

Perhaps for the large fish the capability for low speed, makes possible speeds which are energetically prudent in an ecological sense.

Unfortunately the energy balances for these species are not known, especially in regard to energy expended for energy encountered as prey and in regard to energy conserved by low activity during times of day that feeding does not occur. However, in my view the most consistent explanation for the adaptations that reduce required speeds among larger scombroids and the xiphoids is that the speeds must be energetically prudent; and the larger the fish, the less likely this would be possible without a gas bladder and large lifting hydrofoils. Alternatively, but less likely in my opinion, perhaps Brett's and Hunter's estimates of endurance speeds and Shuleikin's estimate of the most efficient speed for migration are overestimates of the physiological capabilities of large scombroids and xiphoids for sustained swimming.

Larger scombroids are then not able to avail themselves of whatever advantages have been achieved by some smaller species and individuals of scombroids by the loss of a gas bladder. Problems of large size among scombroids become either the possibility of an energetically imprudent basal speed requirement to maintain hydrostatic equilibrium or a loss (Magnuson, 1966b; Aleev, 1969), owing to a large gas bladder, in vertical mobility especially near the sea surface. I have observed *K. pelamis*, a species without a gas bladder, swim vertically upward at burst speeds in the top 10 m of the sea. Large scombroids and xiphoids would be expected to live either (1) deep in the water column where rapid vertical excursions have little effect on gas expansion or (2) immediately below the surface and making no rapid upward excursions. The pressure change experienced in an ascent from 10 m to the surface results in a 100% increase in the volume of an unrestricted gas bladder but an ascent from 100 to 90 m results in an increase in volume of only 10%. Alternatively, (3) to retain rapid vertical mobility, those with gas bladders and living near the surface would require remarkably strong-walled gas bladders that could maintain the gas at greater than ambient pressures. A casual review of the natural history of large scombroids and xiphoids suggests that all three alternatives are evidenced in one form or the other. The most unlikely species would be one with a large, thin-walled gas bladder that also cruised at 10 m below the surface and chased its prey or escaped predation vertically toward the sea surface.

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LITERATURE CITED

ABE, T., AND Y. TAKASHIMA.
1958. Differences in the number and position of two kinds of fin-supports of the spinous dorsal in the Japanese mackerels of the genus *Pneumatophorus*. Jap. J. Ichthyol. 7:1-11.

ALEEV, YU. G.
1963. Funktsional'nye osnovy vneshnego stroeniya ryby (Function and gross morphology in fish). Izd. Akad. Nauk SSSR. Moscow, 245 p. (Translated by Israel Program Sci. Transl., 1969, 268 p., available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA., as TT 67-51391.)

ALEXANDER, R. M.
1967. Functional design in fishes. Hutchinson, Lond. 160 p.
1968. Animal mechanics. Univ. Wash. Press, Seattle, x + 346 p.

BARRETT, I., AND A. R. CONNOR.
1962. Blood lactate in yellowfin tuna, *Neothunnus macropterus*, and skipjack, *Katsuwonus pelamis*, following capture and tagging. [In English and Spanish.] Bull. Inter-Am. Trop. Tuna Comm. 6:231-280.

BARRETT, I., AND A. A. WILLIAMS.
1965. Hemoglobin content of the blood of fifteen species of marine fishes. Calif. Fish Game 51:216-218.

BEARDSLEY, G. L., JR., AND W. J. RICHARDS.
1970. Size, seasonal abundance, and length-weight relation of some scombrid fishes from southeast Florida. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 595, 6 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BREDER, C. M., JR.
1948. Field book of marine fishes of the Atlantic coast from Labrador to Texas; being a short description of their characteristics and habits with keys for their identification. G. P. Putnam's Sons, N.Y., 332 p.

BRETT, J. R.
1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22:1491-1501.

CALKINS, T. P., AND W. L. KLAWE.
1963. Synopsis of biological data on black skipjack, *Euthynnus lineatus* Kishinouye 1920. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:130-146.

CHANG, R. K. C., AND J. J. MAGNUSON.
1968. A radiographic method for determining gas bladder volume of fish. Copeia 1968:187-189.

COLLETTE, B. B., AND R. H. GIBBS, JR.
1963. Preliminary field guide to the mackerel- and tuna-like fishes of the Indian Ocean (Scombridae). Smithson. Inst., Wash., D.C., 48 p.

COLLETTE, B. B., F. H. TALBOT, AND R. H. ROSENBLATT.
1963. The first California record of sierra, *Scomberomorus sierra* Jordan and Starks. Calif. Fish Game 49:53-54.

FITCH, J. E., AND P. M. ROEDEL.
1963. A review of the frigate mackerels (genus *Auxis*) of the world. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1329-1342.

FRASER-BRUNNER, A.
1950. The fishes of the family *Scombridae*. Ann. Mag. Nat. Hist., Ser. 12, 3:131-163.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1966. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish Wildl. Serv., Fish. Bull. 66:65-130.

GODSIL, H. C.
1954. A descriptive study of certain tuna-like fishes. Calif. Dep. Fish Game, Fish Bull. 97, 185 p.
1955. A description of two species of bonito *Sarda orientalis* and *S. chiliensis*, and a consideration of relationships within the genus. Calif. Dep. Fish Game, Fish Bull. 99, 43 p.

GODSIL, H. C., AND R. D. BYERS.
1944. A systematic study of the Pacific tunas. Calif. Div. Fish Game, Fish Bull. 60, 131 p.

GOSLINE, W. A., AND V. E. BROCK.
1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu, 372 p.

HILDEBRAND, S. F.
1946. A descriptive catalog of the shore fishes of Peru. U.S. Natl. Mus. Bull. 189, 530 p.

HUNTER, J. R.
1971. Sustained speed of jack mackerel, *Trachurus symmetricus*. U.S. Fish Wildl. Serv., Fish. Bull. 69:267-271.

IDYLL, C. P., AND D. DE SYLVA.
1963. Synopsis of biological data on the blackfin tuna *Thunnus atlanticus* (Lesson) 1830 (western Atlantic). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:761-770.

IVERSEN, E. S., AND H. O. YOSHIDA.
1957. Notes on the biology of the wahoo in the Line Islands. Pac. Sci. 11:370-379.

JONES, S., AND E. G. SILAS.
1962a. On fishes of the subfamily Scomberomorinae (family Scombridae) from Indian waters. Indian J. Fish. 8:189-206.
1962b. Mackerel from the Andaman Sea. Proc. Symposium on Scombroid Fishes. Mar. Biol. Assoc. India, Sympos. Ser. 1:255-282.

KIKAWA, S.
1963. Synopsis of biological data on bonito *Sarda orientalis* Temminck and Schlegel 1842. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:147-156.

KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ. Tokyo 8:293-475.

KLAWE, W. L., I. BARRETT, AND B. M. H. KLAWE.
1963. Haemoglobin content of the blood of six species of scombroid fishes. Nature (Lond.) 198:96.

LAHILLE, F.
1905. Nota sobre el *Chenogaster holmbergi*. An. Mus. Nac. B. Aires, Ser. 3, 4:461-476.

LAWRENCE, H. R., AND A. H. FLAX.
1954. Wing-body interference at subsonic and supersonic speeds—survey and new developments. J. Aeronaut, Sci. 21:289-329.

MAGNUSON, J. J.
1966a. A comparative study of the function of continuous swimming by scombrid fishes. (Abstr.) Proc. 11 Pac. Sci. Congr. 7:15.
1966b. Continuous locomotion in scombrid fishes. (Abstr.) Am. Zool. 6:503-504.
1969. Swimming activity of the scombrid fish *Euthynnus affinis* as related to search for food. FAO (Food Agric. Organ. U.N.) Fish. Rep. 62:439-451.
1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. Copeia 1970:56-85.

MAGNUSON, J. J., AND J. H. PRESCOTT.
1966. Courtship, locomotion, feeding and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14:54-67.

MARCHAL, E.
1963. Synopsis on the biology of little tuna *Euthynnus alleteratus* (Rafinesque) 1810 (east Atlantic and Mediterranean). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:647-662.

MATSUI, T.
1967. Review of the mackerel genera *Scomber* and *Rastrelliger* with description of a new species of *Rastrelliger*. Copeia 1967:71-83.

MUNRO, I. S. R.
1943. Revision of Australian species of Scomberomorus. Mem. Queensl. Mus. 12:65-95.

NAKAMURA, E. L.
1972. Development and uses of facilities for studying tuna behavior. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Current perspectives in research, Vol. 2, p. 245-277. Plenum Press, N.Y.

NAKAMURA, H., T. KAMIMURA, Y. YABUTA, A. SUDA, S. UEYANAGI, S. KIKAWA, M. HONMA, M. YUKINAWA, AND S. MORIKAWA.
1951. Notes on the life history of the sword-fish, *Xiphias gladius* Linnaeus. Jap. J. Ichthyol. 1:264-271.

NAKAMURA, I., T. IWAI, AND K. MATSUBARA.
1968. A review of the sailfish, spearfish, marlin and swordfish of the world. [In Japanese.] Kyoto Univ., Misaki Mar. Biol. Inst., Spec. Rep. 4, 95 p.

NORMAN, J. R., AND F. C. FRASER.
1948. Giant fishes, whales, and dolphins. 2 ed. Putnam, Lond., 376 p.

OGILBY, J. D.
1954. The commercial fishes and fisheries of Queensland, an essay. Revised and illustrated by T. C. Marshall. Dep. Harbours Mar., Brisbane, 121 p.

OSIPOV, V. G., I. V. KIZEVETTER, AND A. V. ZHURAVLEV.
1964. Tuntsy i mecheobraznye Tikhogo i Indiiskogo Okeanov (Tunas and billfishes of the Pacific and Indian Oceans). Moscow, Izd. Pishch. Prom-st', 74 p. (Prelim. transl. by U.S. Joint Publ. Res. Serv., 1965, 71 p., available U.S. Dep. Commer., Natl. Mar. Fish. Serv., Foreign Fish.-(Transl.), Wash., D.C.

OVCHINNIKOV, V. V.
1970. Mechryba i parusnikovye (Atlanticheskii okean. Ekologiya i funktsional'naya morfologiya) (Swordfishes and billfishes in the Atlantic Ocean). Atl. Nauch-Issled. Inst. Ryb. Khoz. Okeanogr., Kaliningrad, 106 p. (Translated by H. Mills, Israel Program Sci. Transl., 1971, 77 p., available U.S. Dep. Commer., Natl. Tech. Inform. Serv., Springfield, Va., as TT 71-50011.)

POSTEL, E.
1955. Contribution à l'étude de la biologie de quelques *Scombridae* de l'Atlantique tropico-oriental. Ann. Stn. Oceanogr. Salammbô 10, 167 p.
1956. Essai sur la palomette *Orcynopsis unicolor* (Geoffroy Saint-Hilaire, 1809). Bull. Inst. Fr. Afr. Noire (A) 18:1220-1248..

RAYNER, M. D., AND M. J. KEENAN.
1967. Role of red and white muscles in the swimming of the skipjack tuna. Nature (Lond.) 214:392-393.

ROBINS, C. R., AND D. P. DE SYLVA.
1963. A new western Atlantic spearfish, *Tetrapturus pfluegeri*, with a redescription of the Mediterranean spearfish *Tetrapturus belone*. Bull. Mar. Sci. 13:84-122.

ROYCE, W. F.
1957. Observations on the spearfishes of the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:497-554.

SERVENTY, D. L.
1948. *Allothunnus fallai*, a new genus and species of tuna from New Zealand. Rec. Canterbury Mus. 5:131-135.

SHULEIKIN, V. V.
1966. Energetika i skorosti migratsii ryb, del'finov, kitov (Force and speeds of migration of fish, dolphins and whales). Tr. Vses. Nauch-Issled. Inst. Morsk. Ryb. Khoz. 60:27-39. Translated by Indian Natl. Sci. Doc. Centre, New Delhi, 1971, *In* P. F. Moiseev (editor), Biological and oceanographic conditions for the formation of commercial concentrations of fish, p. 26-27, available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-59063.

SILAS, E. G.
1963a. Synopsis of biological data on double-lined mackerel *Grammatorcynus bicarinatus* (Quoy and Gaimard) (Indo-Pacific). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:811-833.
1963b. Synopsis of biological data on dogtooth tuna *Gymnosarda unicolor* (Ruppell) 1838 (Indo-Pacific). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:877-899.

TIEWS, K.
1963. Synopsis of biological data on bluefin tuna *Thunnus thynnus* (Linnaeus) 1758 (Atlantic and Mediterranean). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:422-481.

WALDRON, K. D.
1963. Synopsis of biological data on skipjack *Katsuwonus pelamis* (Linnaeus) 1758 (Pacific Ocean). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:695-748.

WALTERS, V.
1962. Body form and swimming performance in the scombroid fishes. Am. Zool. 2:143-149.
1966. On the dynamics of filter-feeding by the wavyback skipjack (*Euthynnus affinis*). Bull. Mar. Sci. 16:209-221.

WALTERS, V., AND H. L. FIERSTINE.
1964. Measurements of swimming speeds of yellowfin tuna and wahoo. Nature (Lond.) 202:208-209.

WILLIAMS, F.
1960. On *Scomberomorus lineolatus* (C.V.) 1831, from British East African waters (Pisces, Scombridae). Ann. Mag. Nat. Hist., Ser. 13, 3:183-192.
1963. Synopsis of biological data on little tuna *Euthynnus affinis* (Cantor) 1850 (Indian Ocean). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:167-179.
YUEN, H. S. H.
1966. Swimming speeds of yellowfin and skipjack tuna. Trans. Am. Fish. Soc. 95:203-209.

ASYMMETRY ANALYSIS IN FISHES: A POSSIBLE STATISTICAL INDICATOR OF ENVIRONMENTAL STRESS

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ABSTRACT

One of the more difficult tasks in evaluating the possible deleterious effects of multiple toxicants on natural communities is in defining subtle sublethal effects before the onset of chronic morbidity. We reason that before detectable changes in either species diversity or species abundance occur subtle changes must take place in a number of important processes, ranging from molecular to behavioral changes. Unfortunately, changes in these parameters have proven most difficult to detect with current methodology. We, therefore, have been examining the possible use of fluctuating asymmetry as a possible measure of environmental stress.

Fluctuating asymmetry is simply the random deviation from perfect symmetry of any bilateral anatomical character. It is, therefore, a nonspecific measure of developmental perturbation.

Using asymmetry analysis on three species of marine teleost—barred sand bass, *Paralabrax nebulifer*; grunion, *Leuresthes tenuis*; and barred surfperch, *Amphistichus argenteus*—from southern California and Baja California, we have been able to define two possible asymmetry trends, historical and geographic. Asymmetry values are shown to increase as we approach highly populated areas (southern California) both from the north and south and also with time within southern California. Such increases in asymmetry correlate well with the known distribution of various toxicants from this same area.

Biological indices are urgently needed for efficiently assessing the effects of man-induced environmental stresses on the marine environment, a task widely acknowledged as both important and difficult (National Scientific Committee on Oceanography of the NAS-NRC Ocean Affairs Board, 1971). Several general approaches are now being used with mixed results: 1) the documentation of die-offs or sterility, such as results from anoxia, thermal shock, pesticides, industrial wastes, oil spills, etc., 2) the detection and description of anomalies ascribable to microorganisms associated with sewage, 3) the quantification of changes in species diversity and community organization, sometimes attributable to thermal, domestic, or industrial effluents, and 4) population changes in certain indicator species which are themselves either resistant or sensitive to specific pollutants (Wilber, 1969). Many of the above methods have been criticized for their insensitivity, lack of standardization, and for being useful only after the occurrence of significant biotic changes. The method we propose may be a useful and sensitive alternative under certain conditions.

Our approach is morphological and is based on fluctuating asymmetry, the random signed differences between the right and left sides of a bilateral character (Van Valen, 1962). The extent to which deviations from perfect symmetry occur is thought to be an estimate of the regulatory capacity of the developmental system in a particular environment. Our working hypothesis is that asymmetry will be increased under certain kinds of environmental stress due to the failure of homeostatic regulatory mechanisms. Such developmental effects might occur before the concentration of toxicants in waters or food reach levels high enough to cause widespread morbidity. It would be slightly easier to use variation per se, such as estimated by the standard deviation or coefficient of variation of a unilateral char-

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acter, to measure such perturbations, but such variation is complex and probably of little use in measuring developmental homeostasis or stability of individuals within a population (Thoday, 1958; Soulé and Cuzin-Roudy, in press). The recent discovery that morphological variation may be highly correlated with mean heterozygosity based on electrophoretic analysis (Soulé and Yang, in press) reemphasizes this point.

Adams and Niswander (1967) suggested that, "It is possible that an overwhelming environmental stress (i.e., teratogen) could [cause] . . . increased asymmetry." We, therefore, decided to examine fluctuating asymmetry as a possible measure of environmental stress. Previous studies of asymmetry have not emphasized the environmental component (for references see Mather, 1953; Thoday, 1958; Reeve, 1960; Sakai and Shimamoto, 1965). The use of paired structures to analyze bilateral developmental differences in fish was first suggested by Hubbs and Hubbs (1945).

MATERIALS AND METHODS

To field test this hypothesis we chose three species of marine teleost fish—barred sand bass, *Paralabrax nebulifer*; grunion, *Leuresthes tenuis*; and barred surfperch, *Amphistichus argenteus*. These species belong to different families and differ greatly in their life histories. They are also abundant throughout the area of study, they are easily captured, and large collections were available from museums for comparative space and time series analyses.

Barred sand bass are generalized carnivores (Quast, 1968) and probably approach the longevity of kelp bass (*P. clathratus*), which can survive at least 32 years in the wild (Young, 1963). Barred sand bass are also of significant importance to the sport fishing industry in southern California (Pinkas, Oliphant, and Haugen, 1968) and are apparently nonmigratory (Young, 1969). Adults (those fish older than 1 year) live offshore in rock-sand ecotonal areas, except during the spawning season when they migrate short distances to sandy areas to spawn (Turner, Ebert, and Given, 1969). From examination of adults, barred sand bass appear to be secondarily gonochoristic, as are kelp bass (Smith and Young, 1966), and are undoubtedly broadcast spawners.

Grunion are small atherinids that mature in about a year, are thought to be nonmigratory, live only 2 or 3 years, and are found in inshore waters (Walker, 1952). They spawn on sandy beaches during the high tides from late February or March through August or September (Walker, 1952). Grunion lack teeth and it is, therefore, assumed that they feed on small organisms (Frey, 1971).

Finally, barred surfperch are found almost exclusively in the surf zone and feed predominantly on sand crabs, *Emerita analoga*, which constitute roughly 90% of their diet (Carlisle, Schott, and Abramson, 1960). From tagging studies, barred surfperch appear to be nonmigratory (Carlisle et al., 1960). In contrast to barred sand bass and grunion, surfperch are viviparous (Eigenmann, 1894), with an apparent maximum life span of 6 years for males and 9 years for females (Carlisle et al., 1960).

All reference to length in this paper refers to the standard length in millimeters, defined as extending from the anterior notch between the premaxillaries to the end of the hypural plate. Variability is expressed as one standard error (SE) or one standard deviation (S) on either side of the mean.

Character Analysis

Seven characteristics were used for asymmetry analysis:

1. Number of pectoral fin rays: A count of the total number of pectoral fin rays, including the uppermost unbranched ray.

2. Total gill rakers: A total count of rakers and all raker rudiments that could be seen under a dissecting microscope. "Secondary" rakers, which frequently occur in barred sand bass with badly deformed rakers (Valentine and Bridges, 1969), were excluded from the count.

3. Scales above the lateral line: A count started approximately two scale rows in front of the first dorsal fin spine and extending ventral-posteriorly along a natural scale row to the pored lateral line scales.

4. Scales below the lateral line: A count

begun between the first anal fin spine and the vent, extending dorso-anteriorly along a natural scale row to the pored lateral line scales.

5. Pored lateral line scales: A count begun with the first anterior pored lateral line scale, usually located under or adjacent to the opercular series, and extending posteriorly to the end of the hypural plate. When the hypural plate is reached, a straight pin is inserted in the last pored scale counted and pushed through the caudal peduncle. When the scales are counted on the other side of the fish, the pin designates the point at which counting should cease.

6. Length of the dentaries: Measured from the symphysis to a small notch at the posterior edge of the dentary.

7. Length of the posterior lateral projection of the epiotic: Measured from the medial notch defining the projection to the tip of the projection.

Where practical, all characters were counted under a binocular microscope. For specimens too large to fit under a microscope, a magnifying glass was used.

Statistical Analysis

The procedure for meristic (countable and discrete) characters follows. For each individual in a sample, the count taken from the left side is subtracted from the corresponding count on the right to obtain the signed difference. Next, the standard deviation of the signed differences (S_{r-l}) is calculated for each sample. Then, the mean of the character ($\bar{x}_{r+l}$) is calculated for each sample by adding the absolute scores for both sides and dividing by the sample size. Finally, the squared coefficient of asymmetry variation (CV_a^2) for each population is defined as follows:

$$CV_a^2 = \left(\frac{S_{r-l} \times 100}{\bar{x}_{r+l}} \right)^2$$

F tests are employed to test for significant differences in asymmetry. We follow Lewontin (1966) in using the squared coefficient of variation as an analogue to the variance.

To obviate scaling problems associated with growth in morphometric characters (nondiscrete, measurable), each measurement (item) is divided by a suitable "general size" measurement (e.g., we utilize the length of the cranium as the standardizing measurement when studying bilateral bones in the cranial region). Each morphometric measurement is so treated before obtaining the signed difference. The variance of the resulting differences is then treated as if it were a CV_a^2 value.

After the above analyses had been performed on a series of barred sand bass from southern ($N = 74$) and Baja California ($N = 101$), we decided to restrict further asymmetry analyses to total gill raker and pectoral fin ray counts since asymmetry in all of the other characters showed a significant association with asymmetry in these (Table 1). Furthermore, pectoral fin rays and gill rakers are the easiest characters to quantify and appear to be the most accurate counts that can be taken on barred sand bass. For both grunion and barred surfperch only the pectoral fin ray and total gill raker counts were used for asymmetry analysis.

Locality Designations

We consider Point Fermin, the first major point north of the Los Angeles-Long Beach Harbors, to be our pivotal locality. Point Fermin is situated approximately equidistant between Point Conception and the California-Mexico border, the northern and southern boundaries for southern California. The distances between Point Fermin and the other localities mentioned in this paper are indicated in Table 2.

RESULTS

Barred Sand Bass

In our original analyses of barred sand bass asymmetry data, we used all characters previously listed. Results from these analyses are presented in Table 1. For all characters, both meristic and morphometric, asymmetry values for southern California barred sand bass are significantly higher than for Baja California or Mexican barred sand bass.

Of interest is the relation between asymmetry and length. Mexican barred sand bass were

TABLE 1.—Comparison of CV_a^2 values and character means ($\bar{x}_{r+l}$) of barred sand bass from southern California and Baja California.

Character	CV_a^2 values		CV_a^2 values				Character means		
	Southern California	N	Baja California	N	F ratios	F ratio probabilities	Southern California	Baja California	t test probabilities
Dentaries / cranium[1]	[2]0.8056	66	[3]0.4868	66	1.621	<0.05	0.984	1.001	<0.01
LEP / cranium[1]	[2]10.3121	66	[4]5.4020	60	1.908	<0.01	0.546	0.484	<<0.001
Scales above lateral line	[5]8.5488	101	[6]3.8534	74	2.219	<0.001	37.485	37.595	<0.9
Scales below lateral line	[5]6.9209	101	[6]1.6268	74	4.254	<<0.001	74.465	75.189	<0.2
Pored lateral line scales	[5]2.2300	101	[6]0.5427	74	4.107	<<0.001	141.901	139.000	<0.001
Pectoral fin rays	[7]1.9604	295	[8]0.4101	210	4.780	<<0.001	35.068	35.448	<0.001
Total gill rakers	[7]8.3009	295	[8]1.9648	210	4.225	<<0.001	53.139	53.648	<0.1

[1] Variances for dentaries / cranium and lateral epiotic projections (LEP) / cranium × 10^4.
[2] Mean standard length 288.4 ± 6.1 mm (SE).
[3] Mean standard length 293.7 ± 6.5 mm (SE).
[4] Mean standard length 292.9 ± 6.8 mm (SE).
[5] Mean standard length 287.0 ± 4.9 mm (SE).
[6] Mean standard length 293.6 ± 6.5 mm (SE).
[7] Mean standard length 193.6 ± 3.2 mm (SE).
[8] Mean standard length 193.3 ± 4.4 mm (SE).

TABLE 2.—Locality designation and approximate straight-line distance to Point Fermin.

Locality	Miles to Point Fermin
San Simeon	210
Santa Rosa Island[1]	100
Carpinteria	85
Point Fermin	0
Belmont Shore	9
San Clemente	53
San Diego	101
California-Mexico border	116
Bahia San Quintin (Mexico)	270
Bahia Sebastian Vizcaino (Mexico)	435
Turtle Bay (Mexico)	475
Southern Baja California (Mexico)	550-750

[1] Santa Rosa Island is 26 miles to sea from the nearest point of land, which is itself 100 miles from Point Fermin.

grouped into size classes (Table 3). From these data it would appear that in small individuals (< 100 mm) pectoral fin ray asymmetry may decrease as size increases, while gill raker asymmetry may decrease. For gill rakers the trend is probably an effect of incomplete development, character means are always lowest in smaller size classes (Tables 3, 4, 5).

Southern California barred sand bass were likewise grouped into size classes (Table 4). Comparing the data in these two tables (3 and 4) will illustrate three notable differences. First, small southern California fish (0.0-49.9 mm) have higher asymmetry levels than do their Mexican counterparts. Second, pectoral fin ray asymmetry increases with size in southern California barred sand bass, instead of decreasing and plateauing, as in Mexican barred sand bass. Third, the largest southern California fish have asymmetry levels four to five times higher than do Mexican fish. (In southern California barred sand bass the association of asymmetry in both characters with standard length is highly significant, $P < 0.01$, using Kendall's coefficient of concordance; Snedecor, 1956.)

Further analyses of these data suggest that these geographic differences in asymmetry are the consequence of both ontogenetic and historical processes that have been occurring in the southern California population. The possible ontogenetic change is an increase in asymmetry with size (age). The possible historical process is a secular increase in asymmetry. Both hypotheses are sufficient to account for the observed trends. Unfortunately, data are lacking to resolve this problem by straightforward regression analyses. Nevertheless, the following analyses suggest that both processes are operating.

First, the ontogenetic theory is examined by following cohorts (cohort, in this case, being defined as specimens spawned in the same year, regardless of the size or age of the fish at the time of capture). Our only collections containing enough specimens to perform such an analysis are those hatched in 1957, 1958, and 1959

TABLE 3.—CV_a^2 values and character means ($\bar{x}_{r+l}$) by size class of barred sand bass from Baja California.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 49.9	31	44.5 ± 0.8	1.0708	0.7428	35.290	51.613
50- 99.9	32	66.8 ± 2.5	0.7532	1.4556	35.656	53.094
100-149.9	33	115.7 ± 2.1	0.6724	2.3264	35.606	54.364
150-249.9	19	196.9 ± 7.4	0.4220	1.4668	35.316	54.316
250-299.9	36	279.8 ± 2.1	0.4592	2.6348	35.278	54.083
300 and up	59	329.5 ± 3.5	0.4088	2.3332	35.475	54.136

TABLE 4.—CV_a^2 values and character means ($\bar{x}_{r+l}$) by size class of barred sand bass from southern California.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 49.9	19	39.1 ± 1.4	1.3553	5.8338	34.789	50.842
50- 99.9	27	70.6 ± 2.8	0.9405	8.2111	34.852	52.556
100-149.9	80	130.1 ± 1.4	1.8461	6.0791	35.150	52.888
150-199.9	39	162.9 ± 1.6	2.1140	10.7590	35.077	54.846
200-249.9	28	228.5 ± 2.8	1.8782	11.5168	35.321	52.893
250-299.9	70	278.6 ± 1.6	2.8201	7.3304	35.014	53.186
300 and up	32	365.1 ± 7.7	2.3502	11.0300	35.094	53.656

TABLE 5.—CV_a^2 values and character means ($\bar{x}_{r+l}$) for southern California barred sand bass probably hatched in 1957, 1958, and 1959.

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 99.9	21	49.1 ± 3.6	1.2116	4.4860	34.905	50.950
100-199.9	21	146.5 ± 3.8	1.1729	5.5034	35.476	54.952
200-299.9	14	278.9 ± 5.0	1.8465	9.3107	34.928	53.000
300 and up	21	357.7 ± 7.7	1.9322	13.0783	35.048	53.429

(Table 5). These three cohorts were pooled to increase sample size. From Table 5 it is evident that both pectoral fin ray and gill raker asymmetry increased as these particular cohorts aged. The specimens do not exist to perform a similar analysis on Mexican barred sand bass, although we might infer from Table 3 that significant asymmetry changes cease when fish exceed 100 mm.

An historical trend of increasing asymmetry is also indicated. In Figure 1 the appropriate specimens are grouped by their probable dates of hatch. There is evidence for plateauing of this trend since fish hatched after 1966 appear to be no more asymmetric than those hatched in the late fifties. A sampling problem may exist because the collections differ in the average size of specimens examined. This could partially account for the apparent plateauing. To examine this, fish of similar size and age were analyzed (Table 6). The plateau is still apparent, so it is probably real.

To summarize the barred sand bass data, there is evidence for two asymmetry trends in southern California—an increase with size (age) and the other with time. An attempt to partition the asymmetry contributions of these two probable sources by using multiple regression produce inconclusive results due, we think, to the inadequate nature of the samples.

TABLE 6.— CV_a^2 values by year of hatch in the 100.0-199.9 mm size class of barred sand bass from southern California.

Date of hatch[1]	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers
1956 and before	23	127.3 ± 3.1	0.6692	2.4805
1957, 1958, 1959	21	146.5 ± 3.8	1.1791	5.5033
1963, 1964, 1965	51	149.3 ± 2.4	2.7476	10.8313
1966 and later	20	133.4 ± 4.7	2.5353	7.7993

[1] The 1960, 1961, and 1962 year of hatch class of fish were not included in this analysis since $N = 4$.

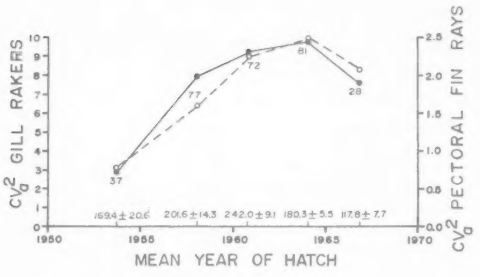

FIGURE 1.—CV_a^2 values for southern California barred sand bass grouped by probable year of hatch. Closed circles, gill rakers; open circles, pectoral fin rays. Numbers on upper abscissa indicate mean length of specimens in samples ± SE. To increase sample sizes fish from several consecutive years of hatch were pooled as follows: up to and including 1956; 1957 through 1959; 1960 through 1962; 1963 through 1965; 1966 and later.

Figure 2 graphically demonstrates how asymmetry values vary with increasing size, both in our Mexican fish and in fish from our southern California cohorts analysis.

Grunion

Only two bilateral meristic counts were made on grunion, the number of pectoral fin rays and total gill rakers. Most grunion were probably not over 2 years old and, hence, were not grouped into classes based on dates of hatch but rather only by dates of collection (Table 7). Our Turtle Bay sample is not large enough to determine asymmetry trends with body size.

The Turtle Bay collection has the lowest CV_a^2 values. Contemporary San Quintin and San Diego collections have statistically increasing CV_a^2 values with time. We employed Kendalls' coefficient of concordance (Snedecor, 1956) on the data in Table 7 to test for asymmetry trends with date of capture for both characters in grunion from Belmont Shore. The results are significant, $0.05 < P < 0.01$, indicating a significant association between year of collection and asymmetry for both characters.

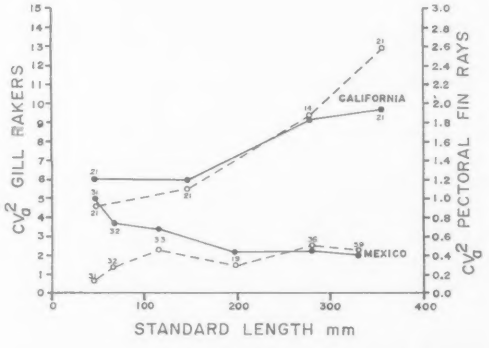

FIGURE 2.—CV_a^2 values for Mexican and California barred sand bass, by standard length. Mexican fish grouped by 50-mm size classes, all years of hatch combined. California fish grouped by 100-mm size classes, only fish hatched in the period 1957-59 included. Dots, gill rakers; open circles, pectoral fin rays. Numbers by data points indicate sample sizes.

Barred Surfperch

For this species, as for grunion, only pectoral fin rays and gill rakers were used in our analyses. From the data presented in Table 8 it can be seen that the barred surfperch data

TABLE 7.—CV_a^2 values and character means ($\bar{x}_{r+l}$) of grunion by locality.

Locality	Date	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
Turtle Bay	1948	49	109.5 ± 1.2	0.7340	0.8344	29.082	68.020
San Quintin	1970	57	126.8 ± 1.5	0.8376	1.5192	28.947	67.057
San Diego	1970	60	137.7 ± 1.6	1.0484	1.3832	28.383	68.000
Belmont Shore	1950-51	51	107.7 ± 1.2	.7364	2.6328	28.451	65.588
Belmont Shore	1963	30	77.8 ± 1.6	1.6376	2.9272	28.533	65.000
Belmont Shore	1966	22	81.9 ± 0.9	3.0388	2.8396	27.864	62.045
Belmont Shore	1968-69	27	97.3 ± 2.8	3.4248	4.2464	27.963	64.444

TABLE 8.—CV_a^2 values and character means ($\bar{x}_{r+l}$) of barred surfperch by locality.

Locality	Date	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
Bahia Sebastian Vizcaino	1952	61	126.1 ± 7.4	0.8028	0.7896	54.597	40.097
Bahia San Quintin	1970-71	44	196.5 ± 6.6	0.7484	1.6328	54.727	39.909
Belmont Shore	1958	73	108.1 ± 3.4	1.2204	2.3268	55.301	38.534
Belmont Shore	1969-70	44	98.2 ± 2.5	2.1660	4.6272	55.364	39.341
Carpinteria	1970	15	164.9 ± 0.5	0.5892	3.6308	53.933	38.667
Santa Rosa Island	1954	56	92.5 ± 7.4	1.5252	1.0700	52.339	38.125
San Simeon	1949	30	112.0 ± 5.4	.4736	1.1476	53.067	38.633

closely approximate the previously presented asymmetry trends for both barred sand bass and grunion. The two oldest collections, Bahia Sebastian Vizcaino and San Simeon, uniformly have low CV_a^2 values. The other relatively old collection, Santa Rosa Island, has moderately high pectoral fin ray asymmetry. The majority of specimens in this collection (37 of 56) are small, ranging between 46 and 77 mm. Barred surfperch, at parturition, are between 42 and 53 mm (Carlisle et al., 1960). A possible explanation for the higher Santa Rosa value is that these small individuals have not yet been exposed to prolonged stabilizing selection. The only other young barred surfperch available for comparison are 18 from Bahia Sebastian Vizcaino (50.1-77.5 mm). Of these 18 specimens, 5 are asymmetric for pectoral fin rays. For our Santa Rosa Island specimens 11 of 37 are asymmetric. Differences are not statistically significant.

To examine the association of asymmetry and size we grouped our three oldest collections (Bahia Sebastian Vizcaino, Santa Rosa Island, San Simeon) and analyzed these collections by size class. Table 9 shows the results of this analysis. Neither gill raker nor pectoral fin ray asymmetry appear to increase with size (age). In Table 8, Figure 3, gill raker data points from Bahia Sebastian Vizcaino, Santa Rosa Island, and San Simeon are connected (solid line) because we feel that these three populations probably represent what might be termed "unperturbed" populations. All three collections are old, all were taken at least 100 miles from Los Angeles and all are probably little exploited by other than natural predators.

Also in Figure 3, all relatively recent collections (San Quintin, 1970-71, Belmont Shore, 1969-70, and Carpinteria, 1970) are connected by a dashed line. The extremely elevated CV_a^2 value for the Belmont Shore collection of 1969-70 should be noted, as well as the high value at Carpinteria.

DISCUSSION

In the discussion of these results we find it necessary to distinguish between two levels of causation. The first is the origin of the asym-

TABLE 9.—CV_a^2 values and character means ($\bar{x}_{r+1}$) by size class of barred surfperch.[1]

Size class (mm)	N	Mean length ± SE	CV_a^2 values: Pectoral fin rays	CV_a^2 values: Total gill rakers	Character means: Pectoral fin rays	Character means: Total gill rakers
0- 74.9	52	58.6 ± 1.1	1.5348	0.8844	52.923	38.904
75-124.9	36	87.4 ± 1.2	0.6924	1.0908	53.639	39.278
125-174.9	34	144.8 ± 2.0	0.6400	1.0008	53.294	38.794
175 and up	26	201.8 ± 3.5	0.9012	0.8728	54.346	39.385

[1] Includes specimens from Bahia Sebastian Vizcaino, San Simeon, and Santa Rosa Island.

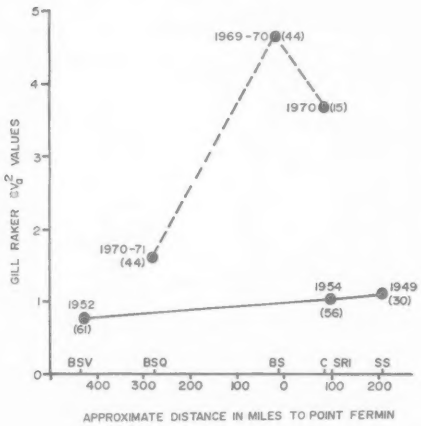

FIGURE 3.—Geographic and historic CV_a^2 trends in barred surfperch. Connected points are more or less "contemporary" samples. Letter codes are as follows: BSV, Bahia Sebastian Vizcaino; BSQ, Bahia San Quintin; BS, Belmont Shore; C, Carpinteria; SRI, Santa Rosa Island; SS, San Simeon. Dates of collection and sample sizes (N) for each collection are as indicated.

metry differences, and the second is the maintenance of these differences. We consider two possible origins: genetic and environmental. The parallel dichotomy with regard to maintenance is that the observed patterns are maintained by natural selection differentials in time and space, or the patterns are maintained by a geographically stable pattern in the distribution of the relevant environmental factor(s). (Other combinations of causative categories exist, but are rejected for lack of evidence and are ignored here.)

The hypotheses explaining our results are grouped into three categories: (A) hypotheses assuming a genetic origin, (B) hypotheses assuming an environmental origin stemming from natural causes, and (C) hypotheses assuming an environmental origin stemming from various pollutants.

Arguments for Category A Hypotheses

All genetic explanations assume the relaxation of stabilizing selection, thus allowing the accumulation of "abnormal" genotypes in the population resulting in an increase in the asymmetry variance of bilateral characters.

Various changes that could bring about such a decrease in the intensity of stabilizing selection in the populations studied are thought to have occurred in the recent past. These changes are of four types: (1) increased cropping of adults by fishermen, (2) a fish population explosion, (3) a decrease in the predator-prey ratio, and (4) an increase in the carrying capacity of the environment. A rapid increase in a population (type 2) depends on a high juvenile recruitment rate. In this respect, the effect of a population explosion is similar to that of increased fishing pressure on adults (type 1), although the former change is usually more transient than fishing pressure changes.

Fishing pressure and the number of fish being caught in southern California are increasing (Frey, 1971). Given that the adult populations of the three species in question have remained stable (there is no evidence to the contrary), then at some stage the removal of adults must be compensated for by increased survival of recruits. One possible consequence of this is an increase in the probability of survival

of abnormal or extreme juveniles. The geographical concordance of asymmetry in these fish and human population density in the area studied is certainly suggestive. Furthermore, asymmetry has apparently been increasing in southern California over the past two decades, as has the number of anglers.

There is evidence that a population explosion of southern California barred sand bass occurred some time during the time period 1957-59. Before this time barred sand bass constituted a minor fraction of the "bass" catch in southern California marine waters ("bass" refers to barred sand bass, kelp bass, and spotted sand bass, *P. maculatofasciatus*), whereas in 1964 they constituted over 50% of the bass catch from private sport fishing vessels (Pinkas et al., 1968). The rapid proliferation of one or two year classes of fish has been known to produce, at least temporarily, phenotypically aberrant cohorts (Whitney, 1961). Similar patterns may be postulated for asymmetry.

A decrease in the predator-prey ratio should have similar effects. One factor maintaining low variability and possibly low asymmetry variances is the elimination of phenotypically and, presumably, genetically deviant individuals via centripetal or stabilizing selection. With less predation there might be higher survival of deviants. Elimination of piscivorous predators may have resulted from increased fishing pressure and reduction in marine piscivorous birds and mammals.

Domestic sewage outfalls in closed bodies of water are known to stimulate productivity (MacKenthun, 1965, for a review). Similar stimulatory effects on marine phytoplankton are to be expected. Increasing primary productivity should lead to higher overall productivity and an increase in the carrying capacity of the environment, particularly near outfalls. An increasing carrying capacity should result in continual growth in the size of the populations of marine organisms associated with outfalls. Increases in asymmetry can easily be correlated with the increasing volume of sewage effluents in southern California. The apparent increase in size of barred sand bass populations can also be so correlated. The higher concentrations of fish near outfalls (reported by fishermen) as opposed to adjacent areas would also be cited. These larger populations of fish may be a direct result of the increased availability of food in areas near outfalls.

Evidence Against Category A Hypotheses

Increased cropping of adult fishes through angler success leading to an increase in asymmetry is a difficult hypothesis to test with the species we have chosen to study. Virtually no data exist on the numbers of grunion and barred surfperch taken yearly. Fisheries statistics for the three basses are pooled by the California Department of Fish and Game, making separation by species most difficult. Most of the bass catch is, however, composed of kelp and barred sand bass. Separating the bass catch into kelp and barred sand bass is difficult.

Prior to 1957 barred sand bass composed a very minor portion of the bass catch (Frey, 1971). From 1947 to 1959 the bass fishery experienced a general decline, reaching a 23-year low of 428,656 bass caught in 1959. Beginning somewhere around the early 1960's barred sand bass began constituting an increasing portion of the bass catch and by 1964, barred sand bass made up roughly half of the bass catch from private fishing vessels (Pinkas et al., 1968). It would, therefore, seem logical that the increase in the bass catch resulted as much from an increase in barred sand bass as from kelp bass. We have seen no information that the proportion of barred sand bass in the bass catch is declining. The total bass catch has been above 1 million for the past 7 years, averaging 1.2 ± 0.109 million individuals from 1963 to 1969. It would, therefore, appear that the barred sand bass population has stabilized.

Recall from Figure 1 that CV_a^2 values in barred sand bass have been increasing from at least 1954 through 1964. During this same period the bass catch passed through a declining phase and then a rapid increase in catch. If fishing pressure were to account partially for these data, we would expect to see relatively stable levels until sometime around 1960, when levels should begin to climb due, on one hand,

to the population explosion of barred sand bass and, on the other, to increased angler success. No such trends are to be found in our data. As previously mentioned, catch data for grunion and barred surfperch are lacking so that it is impossible to examine these species for the possible effects of fishing pressure.

The effects of a population explosion on asymmetry variance should be temporary and will cease when the population stabilizes. The highest asymmetry values should reflect periods of exceptionally high juvenile recruitment.

Our data on probable year of hatch and cohorts analyses show that asymmetry values of barred sand bass are lower in 1957-59 than in later periods. Recall that this is the time when a population explosion of barred sand bass is supposed to have begun. If the asymmetry is genetic and/or congenital, then the low asymmetry of these fish is inconsistent with the above prediction. For our data to support such an hypothesis it would have to be shown that the population of barred sand bass and, for that matter, grunion and barred surfperch, have been continually increasing. Our data do not support this premise. No data exist for either barred surfperch or grunion which can be used as a basis on which to test this premise.

The question of shifting predator-prey ratios is most difficult to analyze. There undoubtedly exist changes in such ratios not only from year to year, but also seasonally. Whether such changes can result in significant shifts in asymmetry variances is unknown. The fact that all three species occupy different habitats, all appear to be undergoing similar asymmetry changes, and all are probably preyed upon by different predators would seem to argue against such a simple cause and effect explanation.

Fish density around outfalls may be high, but this has never been shown to be an effect of the local productivity gradient. A logical alternative is that outfalls, being constructed over sand or muddy bottoms, provide an artificial habitat. Studies by the California Department of Fish and Game (Turner et al., 1969) have shown that artificial reefs in predominantly sandy areas of low relief rapidly attract large assemblages of fish. Barred sand bass were the most frequently observed species and were reported inhabiting artificial reefs within hours after construction terminated.

That larger populations of some species (e.g., barred sand bass) are apparently residing in southern California now than in the past may be ascribed to fluctuations in normal environmental conditions. Furthermore, of the three species studied, only barred sand bass and possibly grunion are likely to be found around sewer outfalls. Barred surfperch are predominantly inshore and seldom venture past the surfzone. They are, therefore, unlikely to be affected as much as are the other two species, unless an increase in primary productivity is widespread. Yet data on asymmetry for all three species are similar.

Arguments for Category B Hypotheses

Naturally occurring, clinally varying abiotic factors would also seem to be a logical source of induced meristic variation since asymmetry increases from Mexico northward. Experimentally, Schmidt (1919, 1920) with brown trout, *Salmo trutta*, and the blenny, *Zoarces viviparus*; Lindsey (1954, 1958) with the paradise fish, *Macropodus opercularis*; Blaxter (1957) with the herring, *Clupea harengus*; Tåning (1952) with the sea trout, *Salmo trutta trutta*; and others have clearly demonstrated that temperature plays a very important role in determining the ultimate meristic counts in a wide range of fishes. Barlow (1961) stated that a good correlation exists between cooler environmental temperatures and higher meristic scores. Other environmental factors such as light intensity (McHugh, 1954, with the grunion), light duration (Lindsey, 1958, with the kokanee, *Oncorhynchus nerka*), oxygen and carbon dioxide tensions (Tåning, 1944, 1952, with the sea trout), and salinity (Heuts, 1947, with the stickleback, *Gasterosteus aculeatus*) have been examined with similar results. About the only factors studied that have not been shown to significantly alter meristic counts are pH and phosphate and nitrate concentrations (Tåning, 1952).

Arguments Against Category B Hypotheses

If asymmetry were to correlate well with mean annual water temperature, we would expect that it should continue to increase with latitude. Our data for barred surfperch are inconsistent with this hypothesis, as are those of Hubbs and Hubbs (1945), who have conducted the only large-scale study of asymmetry encompassing a large latitudinal transect. Hubbs and Hubbs (using a statistic differing from that used here) studied the asymmetry of pectoral fin rays in the Pacific staghorn sculpin, *Leptocottus armatus*, from Sitkalidak Island, Alaska, to Mission Bay, in southern California. Of the 12 populations examined, the highest asymmetry values were from their southern most samples, Anaheim and Mission Bays in southern California (Table 10). The Tau coefficient (Snedecor, 1956), applied to these data, indicate a significant negative asymmetry correlation, $P < 0.05$, with increasing latitude.

Finally, not only are asymmetry values increasing clinally, they also appear to be increasing temporally. We know of no environmental variable showing these continuous trends. Most variables show cyclic fluctuations, whereas our asymmetry values apparently do not.

Arguments for Category C Hypotheses

This hypothesis assumes only that as environmental stress increases so should asymmetry. At this point in time we must leave unspecified what type of stress may produce increases in asymmetry, although preliminary experiments with grunion would seem to indicate that p,ṕ-DDT may have this effect (Valentine and Soulé, 1972).[4] As a first approximation, we might assume that specific ubiquitous pollutants known to interfere with various metabolic processes might logically be suspect. Two such groups of agents are known to occur in the southern California environment (marine, terresterial, and atmospheric), chlorinated hydrocarbons (Risebrough et al., 1967; Schmidt, Risebrough, and Gress, 1971; Duke and Wilson, 1971; Burnett, 1971; Munson, 1972) and heavy metals (Tatsumoto and Patterson, 1963; Brooks, Presley, and Kaplan, 1967; Schroeder, 1971; Galloway, 1972). The distribution of pollutants in southern California waters is similar to the distribution of asymmetry values (Burnett, 1971; Galloway, 1972). This hypothesis would attribute the increases in asymmetry in the species studied to the presence of pollutants and possibly to duration of exposure.

[4] Valentine, D. W., and M. Soulé. 1972. Asymmetry: The effect of p, p′-DDT on the development of fins in the grunion (*Leuresthes tenuis*). Unpublished manuscript.

TABLE 10.—Pectoral fin ray asymmetry in the Pacific staghorn sculpin, *Leptocottus armatus*.[1]

Locality	N	$\bar{x}_{r+l}$	[2] $\frac{100(l+r)}{N}$
Alaska			
Sitkalidak Island	174	38.89	16.67
Admirality Island	104	38.49	22.12
Washington			
Puget Sound	245	38.06	20.41
Grays Harbor	103	37.82	15.53
Oregon			
Nestucca Bay	136	37.94	17.65
California			
Humboldt Bay	221	37.91	19.91
San Francisco Bay Region	223	—	21.97
Elkhorn Slough	145	—	22.75
Morro Bay	218	36.63	20.18
Santa Barbara	397	36.77	20.65
Anaheim Bay	109	37.01	29.36
Mission Bay	119	—	24.37

[1] Data recalculated from Hubbs and Hubbs (1945, Tables VII and VIII).

[2] Hubbs and Hubbs used this statistic to express "the amount of overall asymmetry . . . as a percentage figure in which l and r represent counts that are higher . . . on the left and right sides, respectively, and N is the total number of specimens, symmetrical plus asymmetrical, in the sample."

Arguments Against Category C Hypotheses

The only contraindicative evidence thus far is that if these asymmetries were the result of toxicants, we might expect to find behavioral and reproductive effects. None has as yet been observed, although our preliminary observations on the low viability of first spawned grunion eggs is suspicious (Valentine and Soulé, see footnote 4).

CONCLUSIONS

Several of the explanations presented assume a genetic origin of the asymmetries and involve altered demographic parameters: improved conditions leading to population growth; de-

creased predation resulting in decreased selection; increased fishing pressure. The potential interactions among these processes are manifold. Some are virtually mutually exclusive. For instance a population explosion of predators (including barred sand bass) is inconsistent with a model based on decreased predation. Some models have a superficial complementarity. For instance, a general increase in marine productivity, though resulting in population growth, would not necessarily alter selection against divergent phenotypes. Predator-prey ratios, for instance, might be expected to remain relatively constant.

Most theories that would appear to explain these data are based on a genetic hypothesis. It is not easy to sustain these hypotheses in view of the apparent age-dependency of the asymmetry. Skeletal abnormalities in these same fish (Valentine, in press) show similar temporal and spatial patterns. We tentatively conclude that the environmental stress hypothesis gives the best fit to the data. It is very possible that this approach may be limited in application to the detection of stress induced by agents affecting calcium metabolism, transport, or deposition. Recent experiments, conducted in our laboratory, with the fruit fly, *Drosophila melanogaster*, re-emphasizes this point. We attempted to increase the asymmetry of sternopleural chaeta by raising fruit flies from eggs to adults in culture medium treated with various toxicants (methylmercury chloride, cupric sulfate, tetraethyl lead, and p,p'-DDT). Toxicant concentrations ranged from 1 ppb (part per billion) to lethality and egg concentrations from 1 to 200 per vial. Results, in all instances, were negative.

Asymmetry analysis, if it proves fruitful for measuring environmental stress, has some important benefits. We think such an assay would:

1. permit continuous monitoring of the health of biological communities via periodic checks of specific sensitive organisms;
2. permit the detection of long-term trends (decades) by comparing preserved material with contemporary materials;
3. permit economies to be made in the monitoring of communities and;
4. increase the lead time between the detection of significant biological changes and community morbidity.

SUMMARY

The data presented show two trends, an increase in bilateral asymmetry with time and a consistent spatial pattern. Data for grunion and barred surfperch taken at one locality, Belmont Shore, near Los Angeles, over two decades clearly show increasing temporal asymmetry values. Data from barred sand bass and the other two species show increasing geographic trends from deep Baja California (an area virtually uninhabited) to southern California. Additionally, barred surfperch asymmetry values decrease north of Los Angeles, so that asymmetry is apparently not responding strictly to a latitudinal trend. Several hypotheses were examined, and it is tentatively concluded that environmental toxicant stress is the likeliest explanation.

We believe asymmetry analysis may be developed into a useful tool for examining the sublethal effects of multiple toxicants on natural or laboratory populations. Such analyses are relatively easy to perform and, thus, offer significant advantages over other commonly used assays.

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LITERATURE CITED

ADAMS, M. S., AND J. D. NISWANDER.
1967. Developmental 'noise' and a congenital malformation. Genet. Res. 10:313-317.

BARLOW, G. W.
1961. Causes and significance of morphological variation in fishes. Syst. Zool. 10:105-117.

BLAXTER, J. H. S.
1957. Herring rearing—III The effect of temperature and other factors on myotome counts. Scotl. Home Dep., Mar. Res. 1:1-16.

BROOKS, R. R., B. J. PRESLEY, AND I. R. KAPLAN.
1967. APDC-MIBK extraction system for the determination of trace elements in saline waters by atomic-absorption spectrophotometry. Talanta 14: 809-816.

BURNETT, R.
1971. DDT residues: Distribution of concentrations in *Emerita analoga* (Stimpson) along Coastal California. Science (Wash., D.C.) 174:606-608.

CARLISLE, J. G., JR., J. W. SCHOTT, AND N. J. ABRAMSON.
1960. The barred surfperch (*Amphistichus argenteus* Agassiz) in Southern California. Calif. Dep. Fish Game, Fish Bull. 109, 79 p.

DUKE, T. W., AND A. J. WILSON, JR.
1971. Chlorinated hydrocarbons in livers of fishes from the northeastern Pacific Ocean. Pestic. Monit. J. 5:228-232.

EIGENMANN, C. H.
1894. On the viviparous fishes of the Pacific coast of North America. Bull. U.S. Fish Comm. 12:381-478.

FREY, H. W. (editor)
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, [Sacramento] 148 p.

GALLOWAY, J. N.
1972. Man's alteration of the natural geochemical cycle of selected trace metals. Ph.D. Thesis, Univ. California, San Diego, LaJolla, 162 p.

HEUTS, M. J.
1947. The phenotypical variability of *Gasterosteus aculeatus* (L.) populations in Belgium. Verh. K. Ned. Akad. Wet. Afd. Natuurkd. Tweede Reeks 9:1-63.

HUBBS, C. L., AND L. C. HUBBS.
1945. Bilateral asymmetry and bilateral variation in fishes. Pap. Mich. Acad. Sci., Arts Lett. 30:229-310.

LEWONTIN, R.
1966. On the measurement of relative variability. Syst. Zool. 15:141-142.

LINDSEY, C. C.
1954. Temperature-controlled meristic variation in the paradise fish *Macropodus opercularis* (L.). Can. J. Zool. 32:87-98.
1958. Modification of meristic characters by light duration in kokanee, *Oncorhynchus nerka*. Copeia 1958:134-136.

MACKENTHUN, K. M.
1965. Nitrogen and phosphorus in water. An annotated selected bibliography of their biological effects. U.S. Public Health Serv., 111 p.

MATHER, K.
1953. Genetical control of stability in development. Heredity 7:297-336.

MCHUGH, J. L.
1954. The influence of light on the number of vertebrae in the grunion, *Leuresthes tenuis*. Copeia 1954:23-25.

MUNSON, T. O.
1972. Chlorinated hydrocarbon residues in marine animals of Southern California. Bull. Environ. Contam. Toxicol. 7:223-228.

NATIONAL SCIENTIFIC COMMITTEE ON OCEANOGRAPHY (NASCO) OF THE NAS-NRC OCEAN AFFAIRS BOARD.
1971. (draft). Preliminary report of the task group on major ocean pollutants for the IDOE Marine Environmental Quality Study.

PINKAS, L., M. S. OLIPHANT, AND C. W. HAUGEN.
1968. Southern California marine sportfishing survey: Private Boats, 1964; shoreline, 1965-66. Calif. Dep. Fish Game, Fish Bull. 143, 42 p.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

REEVE, E. C. R.
1960. Some genetic tests on asymmetry of sternopleural chaeta number in *Drosophila*. Genet. Res. 1:151-172.

RISEBROUGH, R. W., D. B. MENZEL, D. J. MARTIN, JR., AND H. S. OLCOTT.
1967. DDT residues in Pacific sea birds: A persistent insecticide in marine food chains. Nature (Lond.) 216:589-590.

SAKAI, K-I., AND Y. SHIMAMOTO.
1965. Developmental instability in leaves and flowers of *Nicotiana tobacum*. Genetics 51:801-813.

SCHMIDT, J.
1919. Racial studies in fishes. III. Diallel crossings with trout (*Salmo trutta* L.). J. Genet. 9:61-67.
1920. Racial investigations. V. Experimental investigations with *Zoarces viviparus* L. C. R. Trav. Lab. Carlsberg 14:1-14.

SCHMIDT, T. T., R. W. RISEBROUGH, AND F. GRESS.
1971. Input of polychlorinated biphenyls into California coastal waters from urban sewage outfalls. Bull. Environ. Contam. Toxicol. 6:235-243.

SCHROEDER, H. A.
1971. Metals in the air. Environment 13:18-24, 29-31.

SMITH, C. L., AND P. H. YOUNG.
1966. Gonad structure and reproductive cycle of the kelp bass, *Paralabrax clathratus* (Girard), with comments on the relationships of the serranid genus *Paralabrax*. Calif. Fish Game 52:283-292.

SNEDECOR, G. W.
1956. Statistical methods applied to experiments in agriculture and biology. 5th ed., Iowa State Press, Ames, 534 p.

SOULÉ, M., AND J. CUZIN-ROWDY.
In press. Aspects of developmental stability in complex morphological characters. Am. Nat.

SOULÉ, M. E., AND S. Y. YANG.
In press. The genetic-phenetic variation correlation. Nature (Lond.)

TÄNING, Å. V.
1944. Experiments on meristic and other characters in fishes. I. Medd. K. Dan. Fisk. Havunders. Fisk. 11 (3), 57 p.
1952. Experimental study of meristic characters in fishes. Biol. Rev. (Camb.) 27:169-193.

TATSUMOTO, M., AND C. C. PATTERSON.
1963. The concentrations of common lead in sea water. Earth Science and Meteorites: North Holland Publ. 1057 (38):167-175.

THODAY, J. M.
1958. Homeostasis in a selection experiment. Heredity 12:401-415.

TURNER, C. H., E. E. EBERT, AND R. R. GIVEN.
1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

VALENTINE, D. W.
In press. Anomalies in marine teleosts. *In* G. Migaki and W. E. Ribeline (editors), Symposium on Fish Pathology. Williams & Wilkins, Balt.

VALENTINE, D. W., AND K. W. BRIDGES.
1969. High incidence of deformities in the serranid fish, *Paralabrax nebulifer*, from Southern California. Copeia 1969:637-638.

VAN VALEN, L.
1962. A study of fluctuating asymmetry. Evolution 16:125-142.

WALKER, B. W.
1952. A guide to the grunion. Calif. Fish Game, 38:409-420.

WHITNEY, R. R.
1961. The bairdiella, *Bairdiella icistius* (Jordan and Gilbert). *In* B. W. Walker (editor), The ecology of the Salton Sea, California, in relation to the sportfishery, p. 105-151. Calif. Dep. Fish Game, Fish Bull. 113.

WILBER, C. G.
1969. The biological aspects of water pollution. Charles C. Thomas, Springfield, Ill., 296 p.

YOUNG, P. H.
1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947-1958. Calif. Dep. Fish Game, Fish Bull. 122, 67 p.
1969. The California partyboat fishery, 1947-1967. Calif. Dep. Fish Game, Fish Bull. 145, 91 p.

DISTRIBUTION OF SAND LANCE, *AMMODYTES* SP., LARVAE ON THE CONTINENTAL SHELF FROM CAPE COD TO CAPE HATTERAS FROM RV *DOLPHIN* SURVEYS IN 1966

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ABSTRACT

Postlarvae of one species of sand lance, which rasembled *Ammodytes marinus* exactly, were collected along the east coast of the United States between Martha's Vineyard, Mass., and Cape Hatteras, N.C. (lat 41° to 35°N), in January-February, April, May, and December 1966. They were more abundant in tows taken at night than in tows taken during the day. Recently hatched specimens (4-8 mm) were more abundant in shallow water. Diurnal migrations are probably related to feeding in all larger size groups.

The greatest abundance of sand lance larvae occurred in winter off the mouths of the principal estuaries (southern New England, Delaware and Chesapeake Bays). Dispersing rapidly offshore, they were taken all the way to the edge of the continental shelf. As they grew, abundance appeared to be directly related to that of plankton organisms, which in turn were somewhat affected by the presence of estuaries along the coast. By mid-May, larvae were not available to us in this region, probably moving to coastal beaches, up into the estuaries, or onto the bottom.

Sand lances, *Ammodytes* sp., are found in great abundance on offshore banks, along the coast, and in estuaries from Greenland to Virginia (Richards, Perlmutter, and McAneny, 1963; Scott, 1968). They are important as a food item for both commercial and sport fish, yet the biology of the sand lances of North America is not well known. Postlarval sand lances commonly occur along the southern New England coast from early December until April (Wheatland, 1956; Richards, 1959, 1965; Pearcy and Richards, 1962; Herman, 1963; Richards et al., 1963; Williams, Richards, and Farnworth, 1964). In New Jersey (Croker, 1965), Delaware Bay (de Sylva, Kalber, and Shuster, 1962), and in the region of Chesapeake Bay (Norcross, Massman, and Joseph, 1961), postlarvae occur from January through April.

In 1966, postlarvae were abundant in collections from four cruises (January-February, April, May, and December) made over 12 transects between the coast and the edge of the continental shelf from Martha's Vineyard to Cape Hatteras. These collections were made by personnel at the Sandy Hook Marine Laboratory, Highlands, N.J., as part of a program to determine the extent to which migratory fishes are associated with estuaries during their early life histories.

METHODS AND MATERIALS

Details of the design of the RV *Dolphin* surveys, collecting methods, station positions, and physical data are included in Clark et al. (1969). From December 1965 through December 1966, a series of 92 stations on 14 transects, from Martha's Vineyard to Cape Lookout, N.C., were sampled every 6 weeks with two Gulf V plankton nets towed simultaneously for 30 min (Figure 1, Table 1). Where water depth permitted, oblique tows were made at two levels:

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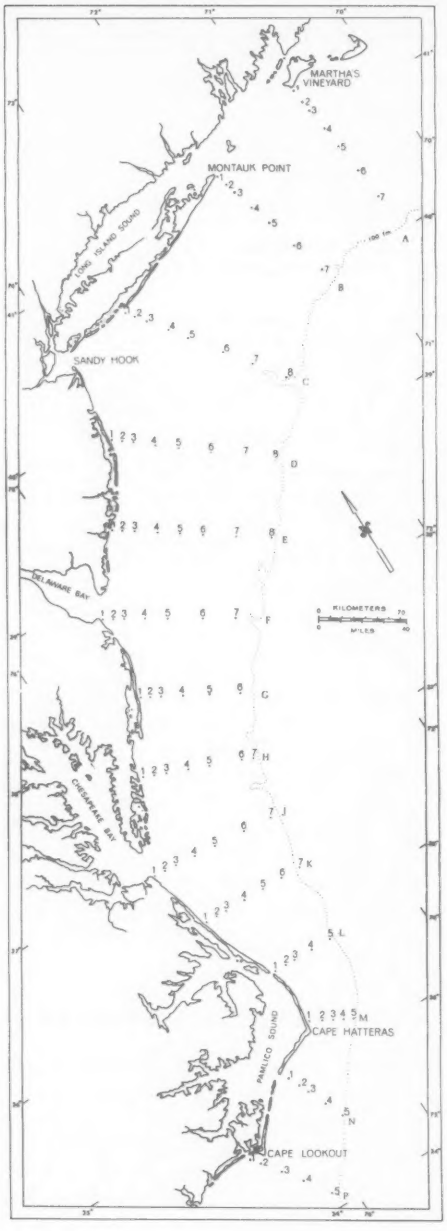

FIGURE 1.—RV *Dolphin* survey, 1965-66. Locations of transects and collecting stations.

TABLE 1.—RV *Dolphin* survey, 1965-66. Transect locations.

Transect	State	Locality
A	Massachusetts	Martha's Vineyard
B	New York	Eastern Long Island
C		Western Long Island
D	New Jersey	Barnegat Inlet
E		Great Egg Inlet
F	Delaware	Cape Henlopen
G	Maryland	Assateague Island
H	Virginia	Eastern Shore
J		Cape Henry
K	North Carolina	Currituck Beach
L		Oregon Inlet
M		Cape Hatteras
N		Ocracoke Inlet
P		Beaufort Inlet

shallow (0 to 15 m) and deep (18 to 33 m). Collections were made during a 24-hr workday on all cruises, so the number of tows by night and by day varied on each transect from cruise to cruise. Cruises were designed to give information on the time and place of occurrence of many species of fish larvae over an extensive geographic area, and sampling was inadequate to estimate mortality or recruitment. For purposes of comparison, numbers of larvae are expressed as the number taken per tow. Zero catches were not included in these computations but are indicated in appropriate figures. A midwater trawl of 6.4-mm cod end mesh used for collecting juvenile fishes did not catch sand lances. This net was not used extensively during the first four cruises in areas where sand lance juveniles would have been expected. Plankton samples were preserved in 5% Formalin,[3] and all fish eggs and larvae were sorted under a microscope. Sand lances were identified, counted, and measured (total length) with an ocular micrometer. No demersal eggs or sand lance larvae with large yolk sacs were collected.

To determine the number of *Ammodytes* species represented in these collections, we checked pigmentation carefully on all specimens. Meristic characters counted were dorsal and anal fin rays and vertebrae. Skeletons of specimens, within the length range of 34 to 60 mm, were prepared by the enzyme presoak method of Ossian (1970). Following 7 to 14

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

days of soaking in "Biz," the vertebrae of a few specimens could be counted.

RESULTS

Appearance and Meristic Character Counts

According to pigmentation and general appearance, all sand lance larvae in these collections are similar to those described by Richards (1965) and listed as *Ammodytes marinus* by Macer (1967). In this group, Macer included *A. hexapterus* and *A. dubius* of the eastern coast of North America which Richards et al. (1963) previously separated.

The number of larvae examined varied among three cruises; some larvae could not be used because of net damage, and others were too small to have developed fin rays or the total complement of vertebrae. The mean, range, and standard deviation of the meristic counts are listed in Table 2 for specimens from each cruise regardless of locality. Although a slight increase in meristic counts was noticeable as the season progressed, it was not significant.

TABLE 2.—Meristic character counts of larval sand lances from three cruises of the RV *Dolphin*, 1966.

Cruises	Anal fin rays	Dorsal fin rays	Vertebrae
January-February:			
Mean	28.38	57.75	—
Standard deviation	1.10	1.73	—
Range	27-30	56-60	—
Number	16	4	0
April:			
Mean	28.95	59.21	67.43
Standard deviation	1.13	1.76	1.83
Range	27-32	55-63	65-71
Number	86	52	30
May:			
Mean	29.47	58.27	69.40
Standard deviation	1.13	1.00	0.87
Range	27-30	55-60	68-70
Number	19	11	5

There was no evidence from pigment patterns, meristic counts, or seasonal abundance of these larvae that we had more than one species of sand lance between December and May south of Cape Cod, Mass. As Reay (1970) pointed out, the specific definitions of *Ammodytes* in the northwest Atlantic are tenuous, so it is presumptuous to be definite in naming species. Variations in appearance and meristic character counts of these postlarvae appeared to be primarily due to the stage of development. Rate of development fluctuates during the different months because of changes in the physical characteristics of the water at the time of hatching and early growth. As shown previously by Richards (1965), individuals in colder water take longer to develop dorsal and anal fin rays and a full set of vertebrae. Specimens collected in spring were more fully developed than those of an equal length taken in winter.

Numbers of Postlarvae in Night and Day Collections

The time of day during which a particular station was occupied varied between cruises; therefore, the diel time factor must be considered before discussing geographical and seasonal distribution of the sand lance larvae.

The greater catch rate of night tows compared to day tows is apparent from Table 3, in which all night collections are separated from all day collections (including dawn and dusk) regardless of location. In general, there was a higher percentage of positive tows at night than during the day. Roughly 34% of the night tows contained larvae, while only 23% of the day tows were positive. When all tows are considered, larvae were more consistently taken at night throughout all the cruises. The mean number of larvae at night dropped from 16/tow in winter to 5.1 and 5.6/tow in April and May, respectively. During the following spawning season, in December, the mean number of larvae per tow at night was just less than 1. A daylight mean of 5.3 larvae/tow in winter dropped to 1.9/tow in April and 0.1/tow in May. None were taken during the day on the cruise of the following December. Thus, a seasonal change in availability was evident in both day and night tows and was due primarily to dispersion, net avoidance, and mortality. Further analysis of the diurnal distribution of the larvae is not warranted by these

TABLE 3.—The number of sand lance larvae taken at night and during the day from four 1966 RV *Dolphin* cruises.

Item	Night					Day[1]				
	Total	Jan.-Feb.	Apr.	May	Dec.	Total	Jan.-Feb.	Apr.	May	Dec.
Tows										
Total	289	77	71	61	80	250	49	70	83	48
Successful	98	43	40	12	3	57	24	27	6	0
Larvae caught	1,684	1,235	362	34	53	402	258	136	8	0
Larvae per tow (all)	5.8	16.0	5.1	5.6	0.7	1.6	5.3	1.9	0.1	0
Ratio night to day (all tows included)	3.6	3.0	2.7	56.0						

[1] Includes tows taken at dawn and dusk.

data. More precise sampling is necessary before conclusions can be drawn concerning diurnal distribution at different depths.

Geographic Distribution

In general, sand lance larvae were most abundant off southern New England and the region off Delaware Bay (Figure 2). They were less common along the northern New Jersey shore and along the Maryland coast to Chesapeake Bay. South of Chesapeake Bay, they decreased steadily in numbers and were not in samples south of Cape Hatteras. Larval distributions for each cruise are shown in Figures 3, 4, 5, and 6 for shallow and deep tows. Physical data for each cruise are related to larval distribution here.

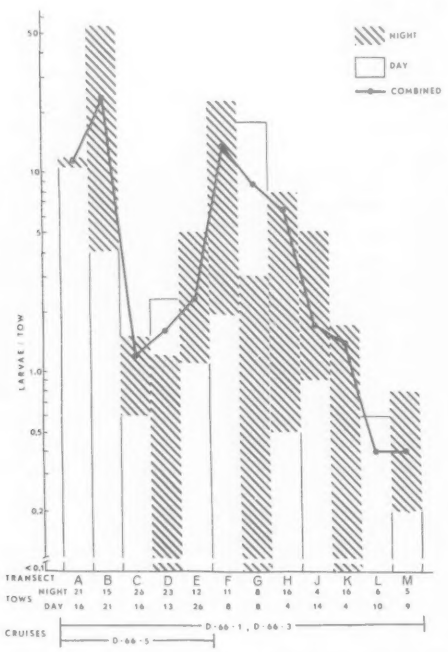

FIGURE 2.—Numbers of sand lance larvae per tow taken in day and night tows by transect.

During the cruise in early December 1965, no larvae occurred in any of the collections. However, during the first week of December 1966, larvae were abundant inshore near Martha's Vineyard and eastern Long Island, N.Y. (Figure 3). They were not found elsewhere in samples from 2 weeks earlier. The catches of larvae in December occurred in water from 8° to 10°C, similar to nearshore temperatures from New Jersey north and offshore of southern New England. Salinity in the area of larval occurrence was 32 to 33‰ over much of the sampling region. Plankton was sparse in the area of capture (<55 to 100 ml/tow).

During the cruise in January-February, larvae occurred in patches throughout the entire area (Figure 4). In shallow tows, none were taken within 15 miles of Long Island (a situation which has occurred before—Richards et al., 1963), off Great Egg Inlet, N.J., at the mouth of Chesapeake Bay, nor off the Oregon Inlet, N.C. Larvae were most abundant 40 miles off Montauk Point, N.Y., eastward to Martha's Vineyard. A second area of abundance occurred within 15 miles of the Maryland coast in the water mass moving southward out of Delaware Bay and extended north 40 miles off the New

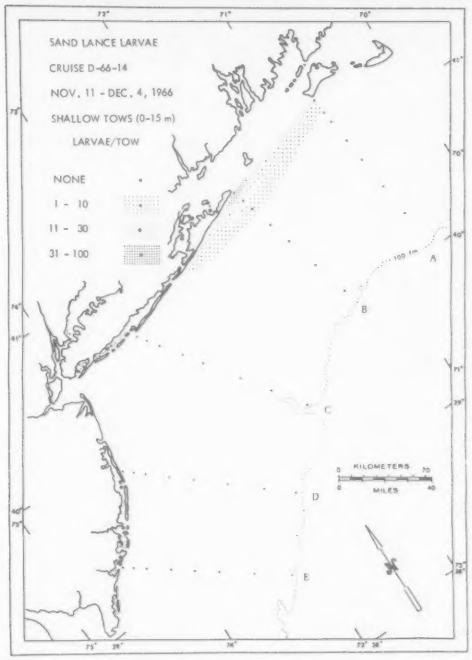

FIGURE 3.—Distribution and abundance of sand lance larvae in the December cruise in shallow tows.

Jersey coast in the latitude of Barnegat Inlet, N.J. Off the mouth of Chesapeake Bay, the greatest numbers occurred during the winter. Norcross et al. (1961) reported a similar seasonal peak in capture rate off Chesapeake Bay during 1960. Data from the deep tows were similar, with the greatest abundance off Montauk Point extending southward offshore. Another group occurred off Delaware Bay, extending in a band to North Carolina (Figure 4). Temperatures in the areas of capture in winter varied from 0° to 6°C and salinities varied from 31 to 33‰. Plankton volumes were less than 100 ml/tow from deep offshore water, but approached 200 ml/tow near the mouths of some estuaries.

During April, sand lances were more widely dispersed and occurred closer to shore from Martha's Vineyard to Assateague Island, Md., than in winter (Figure 5). Similar numbers were taken south to Cape Henry, Va., but further offshore. None occurred farther south, except from a small patch near the surface off Cape Hatteras. As before, larvae were most abundant throughout the water column off the southern New England coast. Only offshore of Maryland were larvae in comparable numbers. Within these same areas, the plankton volumes had increased since winter, providing a good source of food for larvae longer than 5 mm (Covill, 1959). Temperatures had warmed slightly from winter, but most larvae were still taken in water of less than 7°C. The few near Chesapeake Bay and Cape Hatteras were taken in warmer water up to 13°C. Bottom temperature was about 1°C lower than at the surface. Larvae were distributed throughout the salinity range of 31 to 33‰ found in most of the sampled area but were absent in the less saline water off Delaware and Chesapeake Bays. Plankton volumes were similar to those offshore in winter, but those between 10 and 40 miles offshore along Long Island and southern New England showed a slight increase.

By May, larvae occurred only in the northern half of the sampled region, and none were found south of Delaware Bay (Figure 6). In shallow tows, larvae were distributed in two groups—one group within 15 miles of the coast and the other group 5 to 40 miles offshore. Larvae occurred in deep tows only in two areas—inshore off Martha's Vineyard and offshore off western Long Island. Surface temperatures were all above 7°C, and the 10°C isotherm was nearshore off New Jersey and offshore of Maryland. Bottom temperatures were about 3°C cooler than those at the surface. Thus, larvae occurred in waters between 6° and 10°C. Apparently, temperatures south of New Jersey, where larvae were taken earlier in the year, were too warm in May.

Most of the inshore tows from Massachusetts to Delaware were taken at night, which might account for the apparent inshore abundance but not the discontinuous distribution, since intervening stations with no larvae were also sampled at night. Water mass characteristics and plankton distribution may have been important factors in separating these groups. Larval distribution is difficult to relate to salinity distribution. In the past,

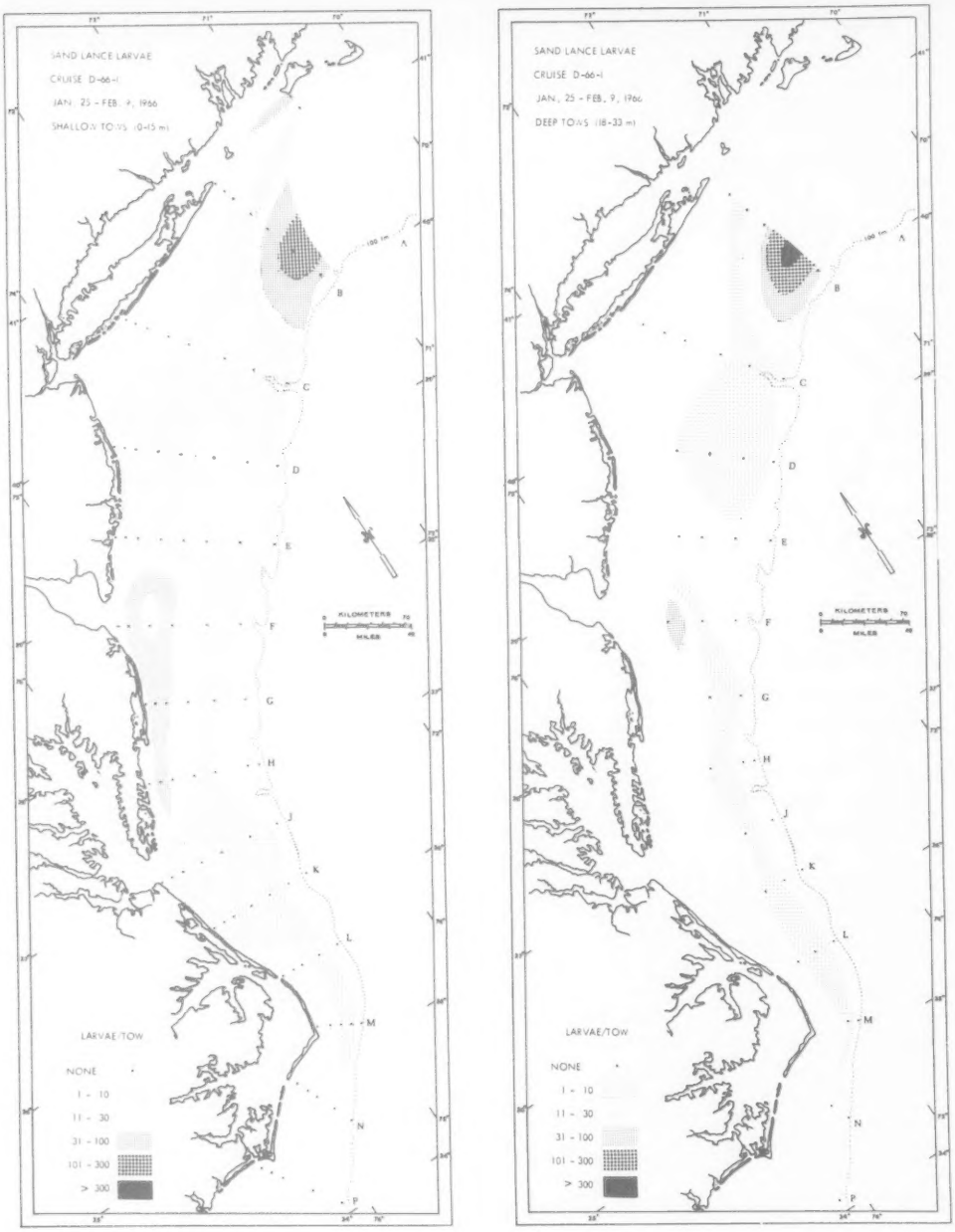

FIGURE 4.—Distribution and abundance of sand lance larvae in the January-February cruise in shallow (left) and deep (right) tows.

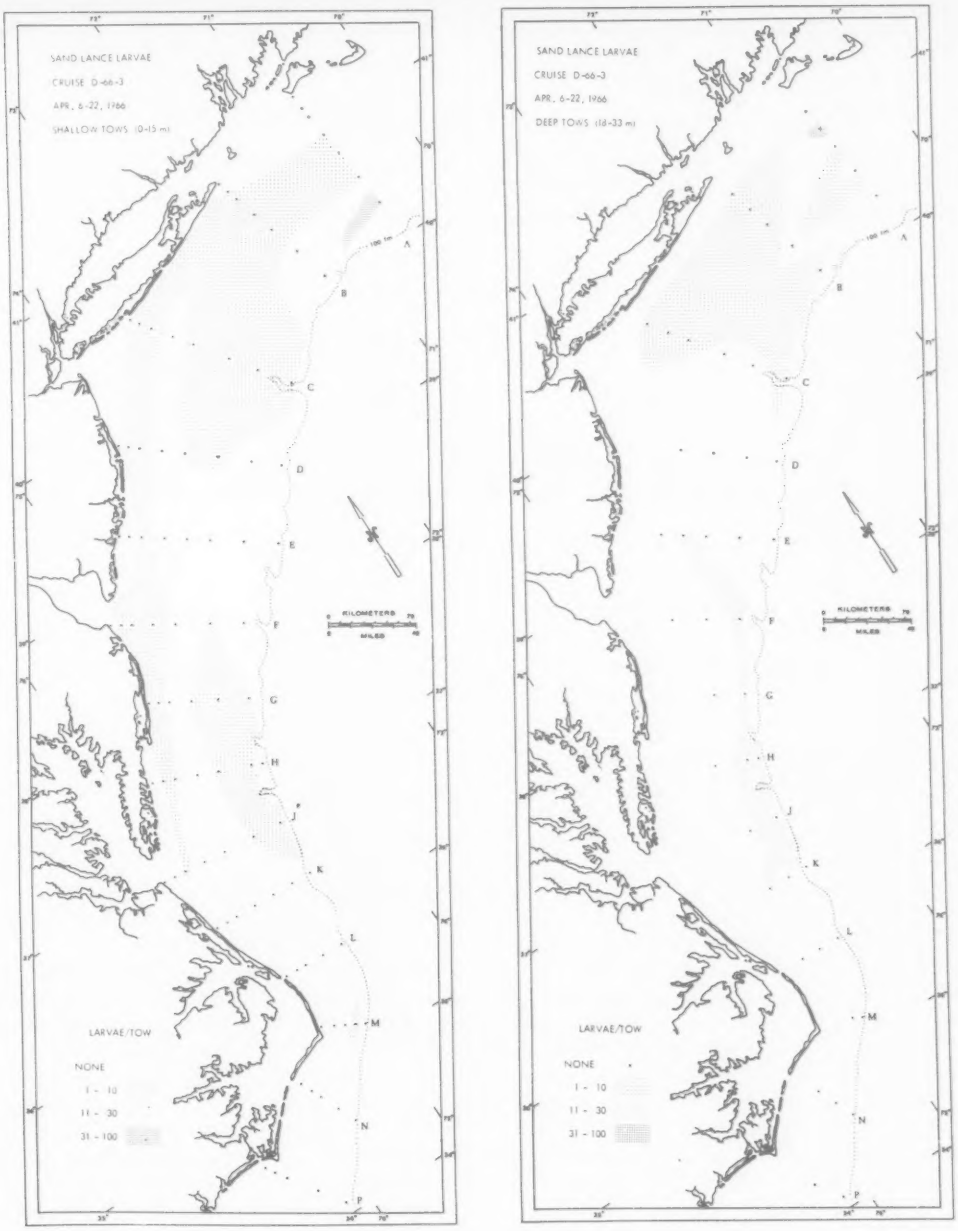

FIGURE 5.—Distribution and abundance of sand lance larvae in the April cruise in shallow (left) and deep (right) tows.

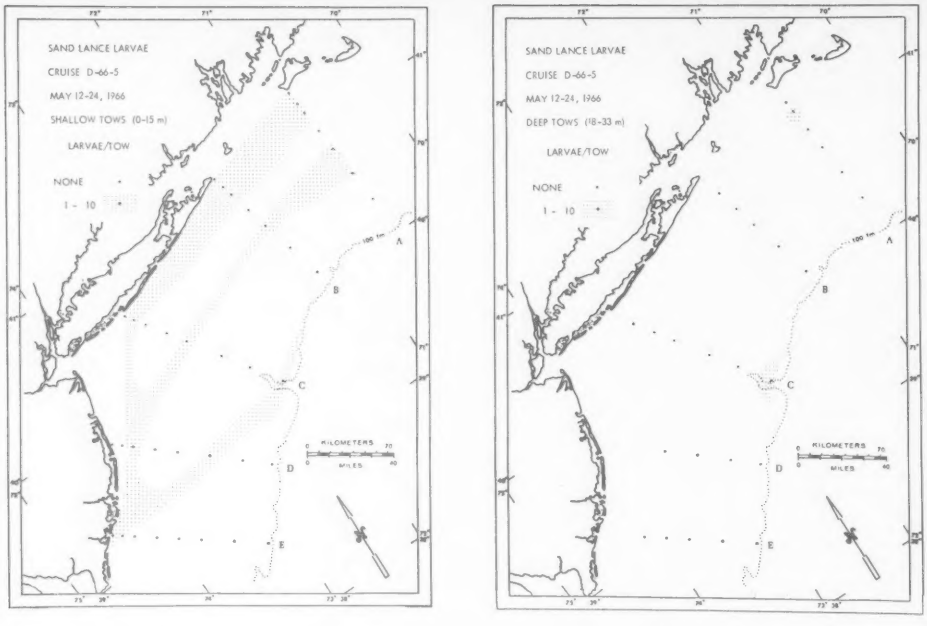

FIGURE 6.—Distribution and abundance of sand lance larvae in the May cruise in shallow (left) and deep (right) tows.

Norcross et al. (1961) found no sand lance larvae off Chesapeake Bay in salinities lower than 30‰, yet Wheatland (1956) found them in Long Island Sound in salinities as low as 24.2‰. Croker (1965) found them in Sandy Hook Bay below 28.6‰, and studies from Delaware Bay indicated larvae occurred in water of 4.3‰ to less than 1.8‰ salinity (Norcross et al., 1961). Plankton distribution was similar to that of the larvae; inshore and offshore volumes of 100 to 200 ml/tow were separated by a low volume strip of 55 to 100 ml/tow. Thus, food was available for both inshore and offshore groups off Long Island and New Jersey. Although plankton abundance was as great off Chesapeake Bay, we found no sand lances in this area.

Distribution and Movements of Larvae of Different Sizes

Figure 7 shows the length frequencies of sand lance larvae for each cruise, and Figures 8, 9, and 10 depict the distributions of five size groups (between 4 and 60 mm). Table 4 gives the depth distribution of these size groups by night and by day. Larvae were seldom taken in deep water tows only, but in many instances they occurred only in tows above 15 m. All larvae collected in December were 4 to 8 mm long.

The total length range generally increased during the spring (Figure 7), and as larvae grew they dispersed away from the coast and decreased in apparent abundance (Figures 8 to 10; Table 4). The greatest number of those of small size occurred inshore at the northern end of the range of these cruises in late fall off Martha's Vineyard and eastern Long Island. Some also appeared in early winter near Delaware Bay. However, lack of many early winter collections, selectivity of the 0.5-mm mesh of the Gulf V sampler, and the hatch from demersal rather than pelagic eggs lowered the chance of sampling the smallest size group in proportion to their abundance. The greatest

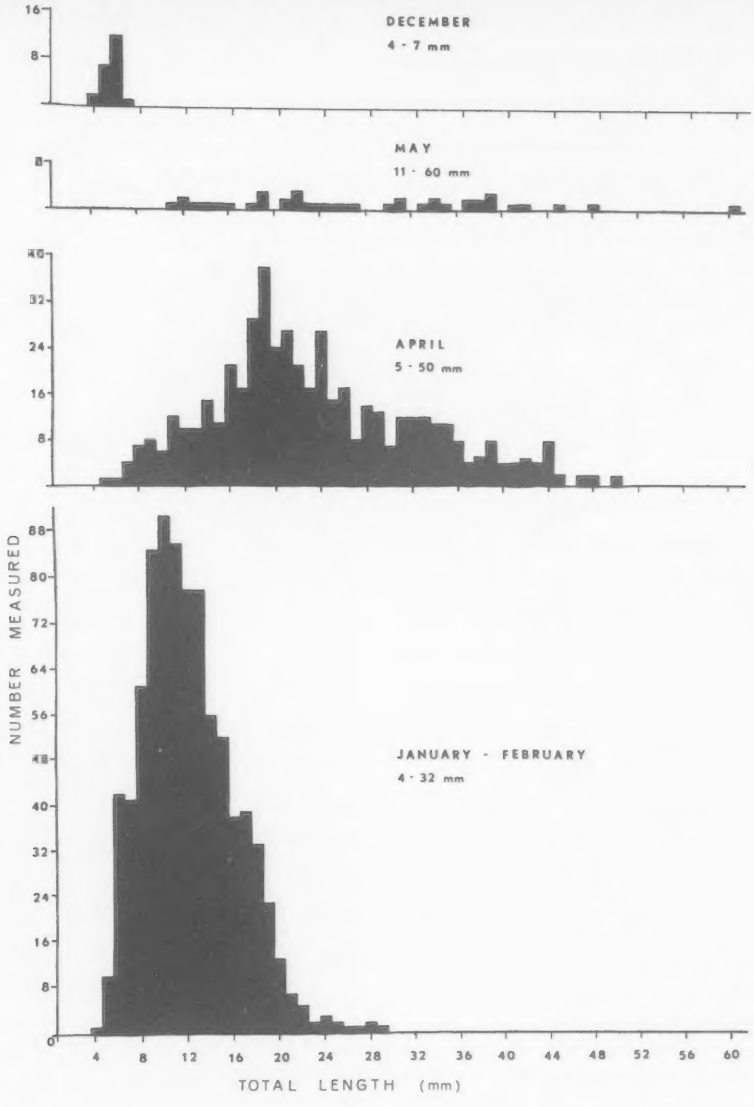

FIGURE 7.—Length frequencies of sand lance larvae from four RV *Dolphin* cruises from January to May and December 1966.

TABLE 4.—Total number of sand lance larvae per positive tow, and the numbers of larvae per tow within five size groups, in shallow and deep tows during the night and during the day, from four 1966 RV *Dolphin* cruises.

Item	Night							Day					
	Shallow				Deep			Shallow			Deep		
	Jan.-Feb.	Apr.	May	Dec.[1]	Jan.-Feb.	Apr.	May	Jan.-Feb.	Apr.	May	Jan.-Feb.	Apr.	May
Number of positive tows	32	27	11	3	11	13	1	18	20	5	6	7	1
Number of larvae:													
Total	697	258	33	53	538	104	1	232	110	7	26	26	1
Per positive tow	21.8	9.6	3.3	17.7	48.9	8.0	1.0	12.9	5.5	1.4	4.3	3.7	1.0
Measured	461	250	33	22	228	103	1	224	109	7	26	26	1
Per tow by size groups:													
4- 7 mm	2.5	—	—	17.7	1.1	0.2	—	3.5	0.2	—	0.2	—	—
8-16	16.4	1.3	0.6	—	40.3	1.6	—	7.2	1.7	—	3.2	1.3	—
17-30	2.9	5.0	1.2	—	7.5	5.3	1.0	2.2	3.0	0.4	1.0	2.1	—
31-50	—	3.2	1.0	—	—	1.0	—	—	0.7	1.0	—	0.3	1.0
>50	—	—	0.2	—	—	—	—	—	—	—	—	—	—

[1] Only category with catches in December.

number of specimens of large size, i.e., above 30 mm, occurred from New Jersey south.

The greatest number of recently hatched larvae—those from 4 to 8 mm—were taken inshore in late fall and early winter off southern New England and in early winter along the Maryland and Virginia coasts (Figure 8). Additional small specimens taken in April off Montauk Point indicate a long spawning season (Figure 9). In winter, they were caught mostly during the day and in shallow water, yet some occurred offshore in deep water south of Montauk Point in winter and off Barnegat Inlet in spring. The absence of this group in May (Figure 10) suggests spawning probably ceased by late March or early April, as previously noted by Norcross et al. (1961) and Wheatland (1956). Distribution of this size group did not seem to be correlated with the distribution of zooplankton organisms. Larvae of this size are still dependent on phytoplankton for food (Covill, 1959).

The size group containing specimens from 8 to 17 mm was most abundant in winter (Figures 7 and 8) and well dispersed along the coast between Montauk Point and south of Chesapeake Bay. By April, larvae in this size group occurred primarily from Martha's Vineyard to Barnegat Inlet. They were still available in that region in May. Larvae of 8 to 17 mm were most abundant at night in deep tows. During the day, they occurred primarily in surface collections, probably because they were feeding there (Table 4). Their horizontal distribution coincided somewhat with that of greatest plankton volumes along the coast during the winter and April cruises. Covill (1959) indicated that sand lances are primarily zooplankton feeders by about 9 mm.

Larvae longer than 17 mm were much less common in midwinter than those of the smaller size groups (Figures 7 and 8). They were primarily offshore off the New Jersey-Delaware Bay area and Chesapeake Bay south to Cape Hatteras, indicating that spawning had begun as early as late November or early December, as previously indicated by Norcross et al. (1961) and Williams et al. (1964). By April, those between 17 and 31 mm were the most abundant group of larvae, being found well offshore off southern New England and inshore off Delaware Bay (Figure 9). None were taken nearshore off Chesapeake Bay; the larvae there were all much larger. In May, a few specimens were taken 10 to 15 miles off southern New England and Long Island (Figure 10).

During winter, there were no specimens larger than 31 mm (Figures 7 and 8). In April, large specimens were common. Off Long Island and New Jersey, they occurred in small

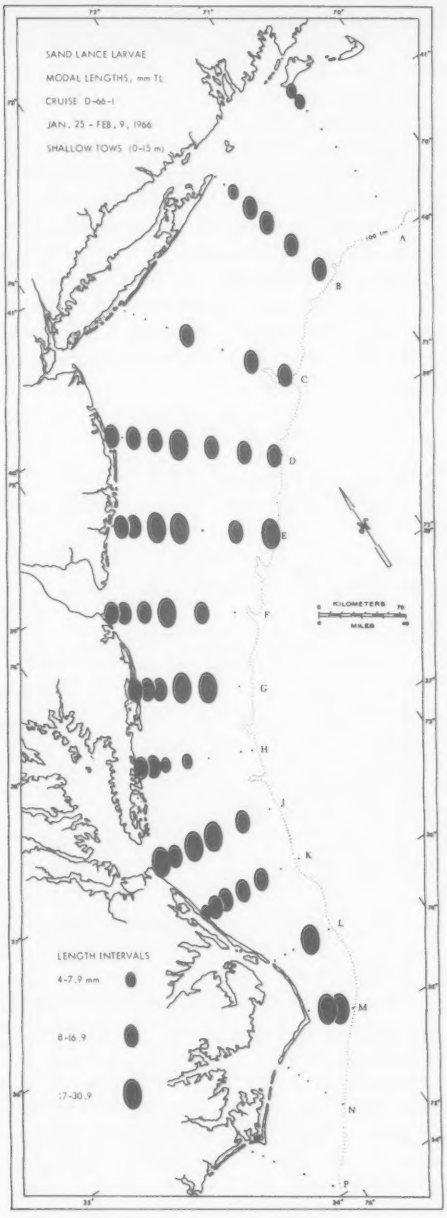

FIGURE 8.—Distribution of sand lance larvae in three length groups from the January-February cruise.

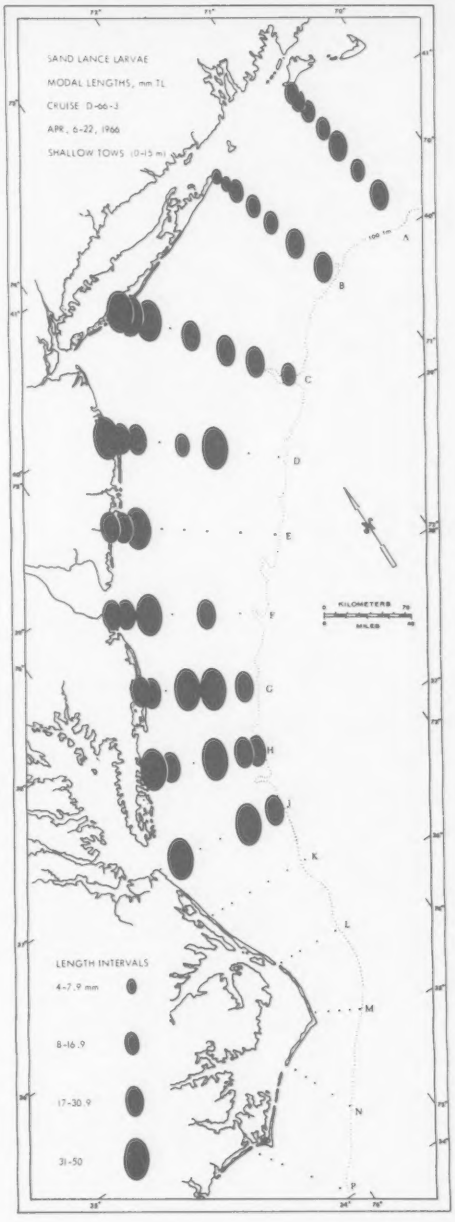

FIGURE 9.—Distribution of sand lance larvae in four length groups from the April cruise.

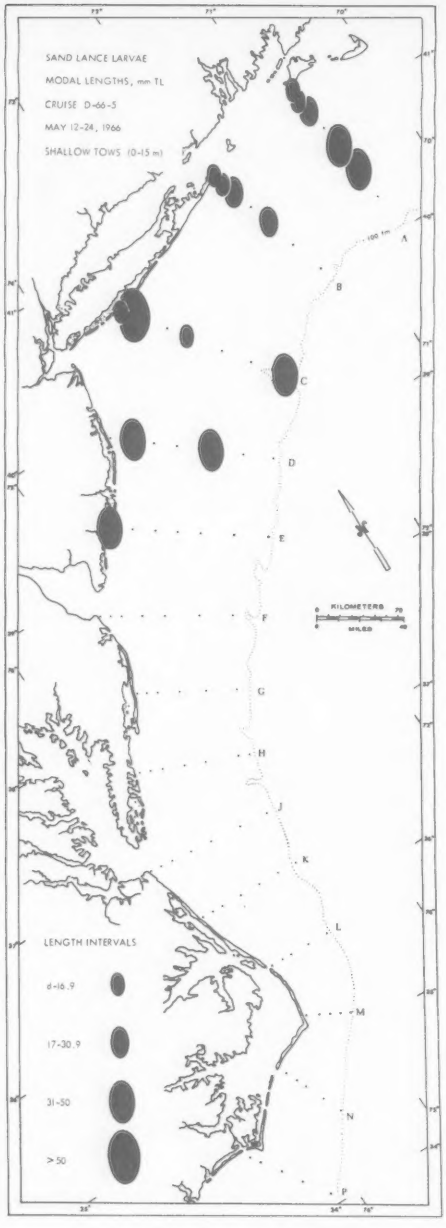

FIGURE 10.—Distribution of sand lance larvae in four length groups from the May cruise.

patches inshore; further south (Figure 9), they extended 20 to 40 miles offshore. During May, specimens larger than 31 mm made up half of those collected (Figure 10). Off southern New England and New York, they were offshore, while along the New Jersey coast they were found close to shore. Their distribution, particularly off Long Island, correlated with that of greatest plankton volumes (Clark et al., 1969). Few larvae larger than 30 mm were collected in deepwater tows either at night or in the daytime. In shallow tows in April and May, the lesser abundance of large larvae by day than at night probably resulted from net avoidance (Table 4).

CONCLUSIONS

Sand lances between lat 35° and 41°N had a long spawning season—from late November to late March. Because larvae became dispersed throughout a large area over a protracted period, the precise location and depth of major spawning areas along the coastal zone were difficult to determine. Nevertheless, it appeared that spawning location was greatly influenced by coastal topography in this region. The greatest numbers of recently hatched individuals occurred in late fall and early winter inshore off southern New England, and Delaware and Chesapeake Bays. In former years within these estuarine regions, spawning occurred in Long Island Sound (Wheatland, 1956; Richards, 1959), Narragansett Bay (Herman, 1963), and Delaware Bay (de Sylva et al., 1962), but apparently neither in Block Island Sound (Merriman and Sclar, 1952) nor inside Chesapeake Bay (Norcross et al., 1961). Judging by our collection of recently hatched individuals in some offshore areas, spawning must occur both offshore and inshore.

Evidence indicated that complicated movements occurred during development of larval sand lances. Hatched from demersal eggs (Williams et al., 1964), eventually larvae were dispersed throughout the water column, where they drifted generally offshore and slightly south. Within this general drift, they tended to move toward the surface during the day for feeding purposes and back into deeper water at night. Their availability to the Gulf V sampler

apparently decreased after they reached 25 mm. During May, larvae and juveniles disappeared from the water column. General migration back to the coast or to the bottom on offshore banks was indicated.

The long spawning season, causing hatching to take place from late November through mid-April, was evidenced by the patchy distribution of small specimens and the multimodal character of length frequencies. Interspersion of groups prevented accurate analysis of growth during the hatching season.

All larvae, regardless of hatching date, had similar melanophore patterns and meristic counts, and resembled postlarval *Ammodytes* previously found from Greenland to Virginia and postlarval *A. marinus* from northern European waters. Differences in meristic character counts probably resulted from temperature effects on development time required to attain adult characteristics.

Data described in this paper show two overlapping areas of larval abundance, indicating that the southern New England sand lances may be separate from those found off Delaware Bay. In addition, earlier evidence suggests that inshore and offshore groups exist (Richards et al., 1963; Scott, 1968). Unfortunately, data from these cruises are not sufficient to determine the definite existence of separate inshore and offshore populations south of Cape Cod. However, it appears that the distribution of all sand lances may be related to estuaries.

LITERATURE CITED

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. Data Rep. I: Northern section, Cape Cod to Cape Lookout. R. V. *Dolphin* cruises 1965-66: Zooplankton volumes, midwater trawl collections, temperatures and salinities. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 28, 132 p.

COVILL, R. W.
1959. Food and feeding habits of larvae and postlarvae of *Ammodytes americanus*, 1952-1955. *In* Oceanography of Long Island Sound, p. 125-146. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).

CROKER, R. A.
1965. Planktonic fish eggs and larvae of Sandy Hook estuary. Chesapeake Sci. 6:92-95.

DE SYLVA, D. P., F. A. KALBER, JR., AND C. N. SHUSTER, JR.
1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper water. Univ. Del. Mar. Lab., Inf. Ser., Publ. 5, 164 p.

HERMAN, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.

MACER, C. T.
1967. Ammodytidae. ICES (Int. Counc. Explor. Sea), Fiches d'identification des oeufs et larves de poissons 2, 6 p.

MERRIMAN, D., AND R. C. SCLAR.
1952. The pelagic fish eggs and larvae of Block Island Sound. *In* Hydrographic and biological studies of Block Island Sound, p. 165-219. Bull. Bingham Oceanogr. Collect., Yale Univ. 13(3).

NORCROSS, J. J., W. H. MASSMANN, AND E. B. JOSEPH.
1961. Investigations of inner continental shelf waters off lower Chesapeake Bay. Part II. Sand lance larvae, *Ammodytes americanus*. Chesapeake Sci. 2:49-59.

OSSIAN, C. R.
1970. Preparation of disarticulated skeletons using enzyme-based laundry "pre-soakers." Copeia 1970: 199-200.

PEARCY, W. G., AND S. W. RICHARDS.
1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. Ecology 43:248-259.

REAY, P. J.
1970. Synopsis of biological data on North Atlantic sand eels of the genus Ammodytes A. tobianus, A. dubius, A. americanus and A. marinus. FAO (Food Agric. Organ. U.N.) Fish. Synop. 82, 42 p.

RICHARDS, S. W.
1959. Pelagic fish eggs and larvae of Long Island Sound. *In* Oceanography of Long Island Sound, p. 95-124. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).

1965. Description of the postlarvae of the sand lance (*Ammodytes*) from the east coast of North America. J. Fish. Res. Board Can. 22:1313-1317.

RICHARDS, S. W., A. PERLMUTTER, AND D. C. MCANENY.
1963. A taxonomic study of the genus *Ammodytes* from the east coast of North America (Teleostei: *Ammodytes*). Copeia 1963:358-377.

SCOTT, J. S.
1968. Morphometrics, distributions, growth, and maturity of offshore sand launce (*Ammodytes dubius*) on the Nova Scotia banks. J. Fish. Res. Board Can. 25:1775-1785.

WHEATLAND, S. B.
1956. Oceanography of Long Island Sound, 1952-1954. VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanogr. Collect., Yale Univ. 15:234-314.

WILLIAMS, G. C., S. W. RICHARDS, AND E. G. FARNWORTH.
1964. Eggs of *Ammodytes hexapterus* from Long Island, New York. Copeia 1964:242-243.

APPENDIX TABLE - R.V. DOLPHIN 1965-66 ICHTHYOPLANKTON SURVEY. DATA ASSOCIATED WITH GULF V CATCHES OF SAND LANCE LARVAE.

CRUISE STAT. D66 1	TOW DEPTH (M)	LARVAE NUMBER TOTAL	LARVAE NUMBER MEAS.	LARVAE LENGTHS (MM TL) MEAN	LARVAE LENGTHS (MM TL) RANGE	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	TEMPERATURE (C) RANGE	TEMPERATURE (C) MEAN	TEMPERATURE (C) SURF.	TEMPERATURE (C) BOT.	THERMOCLINE DEGREE	THERMOCLINE DEPTH (M)	SALINITY (O/OO) RANGE	SALINITY (O/OO) MEAN
A 1	0- 6	50	50	8.9	5.5 20.8	26 1	1627	DUSK	16	1.1	1.1	1.1	1.1	1.1	NONE	-	32.3 32.3 32.3
A 2	0-15	27	27	10.6	6.3 23.2	26 1	1729	NIGHT	33	0.8	0.9	0.9	0.8	0.9	NONE	-	32.4 32.4 32.4
B 3	0-15	21	21	9.2	5.8 14.5	26 1	0429	NIGHT	48	3.2	3.2	3.2	3.2	3.2	NONE	-	32.3 32.3 32.3
B 4	0-15	1	1	11.8	11.8 11.8	26 1	0254	NIGHT	60	4.1	4.1	4.1	4.1	4.1	NONE	-	32.3 32.3 32.3
B 4	18-33	13	13	10.3	5.5 14.6	26 1	0254	NIGHT	60	4.1	4.1	4.1	4.1	4.1	NONE	-	31.9 32.3 32.2
B 5	0-15	37	36	11.5	7.3 16.3	26 1	0115	NIGHT	73	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.5 32.4
B 5	18-33	25	23	11.5	6.9 15.2	26 1	0115	NIGHT	73	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.4 32.4
B 6	0-15	237	57	10.4	6.5 17.5	25 1	2347	NIGHT	80	4.9	4.9	4.9	4.9	4.9	NONE	-	32.3 32.3 32.3
B 6	18-33	344	73	11.0	7.0 20.6	25 1	2347	NIGHT	80	4.9	4.9	4.9	4.9	4.9	NONE	-	32.3 32.4 32.3
B 7	0-15	69	51	12.1	9.6 16.4	25 1	2144	NIGHT	89	4.8	4.8	4.8	4.8	4.8	NONE	-	32.3 32.4 32.4
B 7	18-33	52	52	11.1	8.5 14.6	25 1	2144	NIGHT	89	4.8	4.8	4.8	4.8	4.8	NONE	-	32.4 32.5 32.4
C 5	0-15	2	2	13.5	13.0 14.0	3 2	2208	NIGHT	48	3.8	3.8	3.8	3.8	3.8	NONE	-	32.4 32.6 32.5
C 7	0-15	4	4	14.4	12.3 17.4	4 2	0220	NIGHT	67	4.7	5.0	4.8	4.7	7.1	WEAK	47-56	32.6 32.7 32.6
C 7	18-33	6	6	12.9	10.0 17.0	4 2	0220	NIGHT	67	5.0	5.0	5.0	4.7	7.1	WEAK	47-56	32.6 32.8 32.7
C 8	0-15	4	4	13.8	12.9 15.3	4 2	0408	NIGHT	110	5.8	5.8	5.8	5.8	7.8	WEAK	83-88	33.1 33.3 33.2
D 1	0- 6	4	3	13.2	11.0 15.6	4 2	1729	NIGHT	16	0.8	0.9	0.9	0.8	0.9	NONE	-	31.8 31.9 31.9
D 3	0-15	1	1	13.0	13.0 13.0	4 2	1910	NIGHT	25	1.9	1.9	1.9	1.9	1.9	NONE	-	32.7 32.8 32.7
D 4	0-15	1	1	12.2	12.2 12.2	4 2	2028	NIGHT	27	2.4	2.4	2.4	2.4	2.4	NONE	-	32.8 33.0 32.9
D 5	0-15	1	1	21.2	21.2 21.2	4 2	2220	NIGHT	37	2.9	2.9	2.9	2.9	2.9	NONE	-	32.9 33.1 32.9
D 5	18-24	1	0	20.0	20.0 20.0	4 2	2220	NIGHT	37	2.9	2.9	2.9	2.9	2.9	NONE	-	33.3 33.5 33.5
D 6	0-15	19	19	14.4	12.0 17.8	4 2	1210	DAY	50	3.2	3.2	3.2	3.2	3.1	NONE	-	32.6 32.7 32.6
D 6	18-33	2	2	14.6	13.0 16.3	4 2	1210	DAY	50	3.1	3.1	3.1	3.2	3.1	NONE	-	32.7 33.1 32.9
D 7	0-15	2	2	13.1	12.2 14.0	4 2	1016	DAY	70	4.8	4.8	4.8	4.8	7.1	WEAK	47-55	32.9 33.3 33.0
D 7	18-33	5	5	14.5	13.4 17.4	4 2	1016	DAY	70	4.8	4.9	4.8	4.8	7.1	WEAK	47-55	33.1 33.3 33.1
D 8	0-15	2	2	16.6	15.5 17.8	4 2	0827	DAY	110	4.8	5.0	4.9	4.8	7.2	WEAK	91-99	33.0 33.2 33.1
E 2	0- 6	2	2	15.3	13.4 17.2	5 2	0415	NIGHT	17	-1.4	-1.3	-1.3	-1.4	-1.2	NONE	-	31.6 31.7 31.7
E 3	0- 6	9	9	14.5	7.3 17.5	5 2	0508	NIGHT	20	-0.5	-0.5	-0.5	-0.5	-0.5	NONE	-	31.0 33.2 32.3
E 4	0-15	1	1	18.0	18.0 18.0	5 2	0635	DAWN	30	1.3	1.3	1.3	1.3	1.3	NONE	-	32.5 33.3 32.9
E 5	0-15	1	1	24.0	24.0 24.0	5 2	0804	DAY	37	2.9	2.9	2.9	2.9	2.9	NONE	-	32.6 33.3 32.8
E 7	0-15	22	22	13.5	5.9 22.0	5 2	1126	DAY	66	4.8	4.9	4.8	4.8	6.4	NONE	-	33.6 34.0 33.9
E 8	0-15	1	1	17.1	17.1 17.1	5 2	1326	DAY	121	5.6	5.6	5.6	5.6	5.6	NONE	-	33.6 33.6 33.6
F 2	0- 6	7	7	13.7	10.8 16.4	6 2	0520	NIGHT	22	-1.6	-1.6	-1.6	-1.6	-1.3	NONE	-	30.7 31.8 31.2
F 3	0-15	90	59	13.5	10.3 20.5	6 2	0359	NIGHT	24	-1.4	-0.6	-1.2	-1.4	0.5	NONE	-	31.1 32.4 31.6
F 4	0-15	25	24	14.9	10.3 20.4	6 2	0242	NIGHT	26	0.7	0.9	0.8	0.8	0.8	NONE	-	32.6 33.2 32.7
F 5	0-15	32	30	16.4	12.5 19.6	6 2	0108	NIGHT	34	1.5	1.8	1.7	1.6	1.5	NONE	-	32.6 33.2 33.0
F 5	18-24	84	47	16.9	12.6 21.8	6 2	0108	NIGHT	34	1.5	1.5	1.5	1.6	1.5	NONE	-	33.2 33.4 33.3
F 5	0-15	3	3	14.9	12.5 16.4	5 2	2246	NIGHT	52	5.1	5.1	5.1	5.1	5.1	NONE	-	33.3 34.3 33.7
F 6	18-33	1	1	17.2	17.2 17.2	5 2	2246	NIGHT	52	5.1	5.1	5.1	5.1	5.1	NONE	-	33.8 34.1 34.0
G 1	0- 6	28	28	9.6	4.9 21.4	6 2	0946	DAY	13	-0.1	-0.1	-0.1	-0.1	-0.1	NONE	-	32.5 32.5 32.5
G 2	0- 6	60	50	11.9	6.9 22.7	6 2	1046	DAY	16	0.8	0.8	0.8	0.8	0.8	NONE	-	33.3 33.3 33.3
G 3	0-15	33	33	12.9	5.4 19.1	6 2	1147	DAY	21	1.1	1.2	1.2	1.1	1.1	NONE	-	33.3 33.5 33.4
G 4	0-15	14	13	15.7	12.2 18.9	6 2	0103	NIGHT	27	2.6	2.7	2.6	2.6	2.8	NONE	-	32.7 33.3 33.0
G 5	0-15	1	1	17.9	17.9 17.9	6 2	1428	DAY	52	3.6	3.7	3.6	3.6	4.3	NONE	-	33.0 33.2 33.1
G 5	18-33	12	12	11.8	9.6 18.0	6 2	1428	DAY	52	3.9	4.1	4.0	3.6	4.3	NONE	-	33.4 33.9 33.7
G 6	18-33	1	1	16.9	16.9 16.9	6 2	1611	DAY	86	5.3	5.5	5.4	5.5	5.3	NONE	-	34.2 34.5 34.3
H 1	0- 3	15	15	10.9	5.5 18.6	7 2	0253	NIGHT	11	-0.2	1.4	-0.2	-0.2	0.2	NONE	-	31.5 31.7 31.6
H 2	0- 6	47	45	10.1	6.0 17.7	7 2	0200	NIGHT	16	0.5	0.7	0.6	0.5	0.7	NONE	-	31.6 32.0 31.8
H 3	0- 6	13	13	14.3	6.3 22.2	7 2	0059	NIGHT	22	1.5	1.6	1.6	1.5	1.6	NONE	-	32.2 32.4 32.3
H 4	0-15	11	11	14.7	5.0 25.5	6 2	2332	NIGHT	27	2.8	2.8	2.8	2.8	2.8	NONE	-	32.7 33.0 32.9
H 5	18-24	3	3	16.9	15.5 18.5	6 2	2206	NIGHT	35	4.7	4.7	4.7	4.5	4.7	NONE	-	33.5 33.5 33.5
J 2	0- 6	1	1	20.2	20.2 20.2	7 2	0812	DAY	12	0.6	0.6	0.6	0.6	0.6	NONE	-	30.0 30.4 30.2
J 3	0- 6	3	3	11.1	7.8 13.6	7 2	0906	DAY	12	1.1	1.2	1.2	1.1	1.2	NONE	-	31.5 31.7 31.6
J 4	0-15	1	1	19.0	19.0 19.0	7 2	1030	DAY	20	2.4	2.6	2.4	2.6	2.4	NONE	-	32.3 32.7 32.6
J 5	0-15	2	2	21.5	20.8 23.1	7 2	1143	DAY	26	3.5	3.6	3.5	3.6	3.5	NONE	-	32.9 33.0 33.0
J 6	0-15	3	3	17.2	14.1 19.0	7 2	1321	DAY	35	5.1	5.4	5.1	5.4	5.3	NONE	-	33.4 33.6 33.5
J 6	18-24	2	2	12.1	5.8 18.4	7 2	1321	DAY	35	5.1	5.3	5.2	5.4	5.3	NONE	-	33.6 33.7 33.6
K 1	0- 6	1	1	6.6	6.6 6.6	8 2	0138	NIGHT	15	1.5	1.6	1.5	1.6	1.5	NONE	-	30.9 31.2 31.1
K 2	0-15	4	4	15.0	11.6 17.8	8 2	0038	NIGHT	25	1.5	1.9	1.6	1.8	2.1	NONE	-	31.2 32.1 31.6
K 3	0-15	3	3	19.7	16.7 24.0	7 2	2332	NIGHT	22	3.4	3.8	3.5	3.8	3.4	NONE	-	32.6 32.6 32.6
K 4	0-15	4	4	22.0	14.0 27.8	7 2	2220	NIGHT	31	4.1	4.1	4.1	4.1	4.1	NONE	-	32.6 32.8 32.7
K 5	0-15	6	6	19.7	16.8 21.9	7 2	2101	NIGHT	34	5.1	5.1	5.1	5.1	5.2	NONE	-	33.3 33.3 33.3
K 5	18-24	8	8	18.8	13.5 29.9	7 2	2101	NIGHT	34	5.1	5.1	5.1	5.1	5.2	NONE	-	33.3 33.3 33.3
L 4	0-15	2	2	25.0	17.6 32.5	8 2	1050	DAY	48	5.0	5.1	5.1	5.1	4.8	NONE	-	32.8 32.9 32.9
L 4	18-33	4	4	22.9	14.6 28.1	8 2	1050	DAY	48	4.8	4.9	4.8	5.1	4.8	NONE	-	33.0 33.0 33.0
M 3	0- 6	1	1	22.1	22.1 22.1	8 2	1822	NIGHT	20	3.9	3.9	3.9	3.9	4.0	NONE	-	32.3 32.3 32.3
M 4	0-15	2	2	22.0	20.0 24.0	8 2	1915	NIGHT	42	5.3	5.4	5.3	5.4	5.3	NONE	-	32.2 33.2 32.7
M 4	18-33	1	1	18.7	18.7 18.7	8 2	1915	NIGHT	42	5.3	5.3	5.3	5.4	5.3	NONE	-	33.0 33.1 33.1

APPENDIX TABLE -- CONTINUED

CRUISE STAT. D66 3	TOW DEPTH (M)	LARVAE NUMBER TOTAL	LARVAE NUMBER MEAS.	LARVAE LENGTHS (MM TL) MEAN	LARVAE LENGTHS (MM TL) RANGE	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	TEMPERATURE (C) RANGE	TEMPERATURE (C) MEAN	TEMPERATURE (C) SURF.	TEMPERATURE (C) BOT.	THERMOCLINE DEGREE	THERMOCLINE DEPTH (M)	SALINITY (0/00) RANGE	SALINITY (0/00) MEAN
A 1	C- 6	13	13	15.3	8.2 28.7	6 4	1757	DUSK	23	3.6	3.6	3.6	3.6	3.7	NONE	-	31.6 31.7 31.6
A 2	0-15	18	15	23.8	8.9 47.4	6 4	1911	NIGHT	36	3.3	3.5	3.5	3.5	3.C	NONE	-	31.7 32.1 32.0
A 3	0-15	26	26	17.5	8.4 35.7	6 4	211C	NIGHT	47	3.4	3.5	3.5	3.5	3.C	NONE	-	32.0 32.3 32.1
A 3	18-33	20	19	15.C	5.6 28.7	6 4	2110	NIGHT	47	3.0	3.4	3.1	3.5	3.C	NONE	-	29.1 32.3 30.1
A 4	0-15	10	10	19.4	9.3 29.3	6 4	223R	NIGHT	51	3.4	3.7	3.6	3.8	2.8	NONE	-	31.9 32.5 32.2
A 4	18-33	35	35	21.5	10.9 34.4	6 4	223R	NIGHT	51	2.8	3.3	3.0	3.6	2.8	NONE	-	29.4 32.4 30.5
A 5	0-15	1	1	18.5	18.5 18.5	7 4	0025	NIGHT	62	3.6	3.7	3.7	3.7	2.7	NONE	-	32.0 33.4 33.0
A 5	18-33	2	2	17.5	13.5 21.6	7 4	0029	NIGHT	62	3.0	3.5	3.5	3.7	2.7	NONE	-	33.2 33.6 33.4
A 6	0-15	5	5	22.3	15.6 35.5	7 4	0208	NIGHT	73	3.4	3.7	3.6	3.7	2.7	NONE	-	32.4 33.2 32.7
A 7	0-15	73	7C	20.6	13.4 31.3	7 4	0355	NIGHT	111	3.4	3.6	3.5	3.6	3.5	NONE	-	33.1 33.5 33.3
A 7	18-33	23	23	21.6	16.9 40.1	7 4	0355	NIGHT	111	2.9	3.3	3.2	3.6	3.5	NONE	-	33.5 33.8 33.6
B 1	C- 6	11	1C	13.5	6.8 26.3	7 4	165C	DAY	24	4.7	4.7	4.7	4.7	4.7	NONE	-	30.3 30.9 30.6
B 2	0-15	10	10	13.5	7.6 22.9	7 4	1556	DAY	39	6.2	6.6	6.4	6.4	6.1	NONE	-	31.7 32.2 32.1
B 3	C-15	4	4	14.2	12.8 15.7	7 4	1455	DAY	52	4.8	5.C	4.9	5.C	4.7	NONE	-	31.4 32.1 32.0
B 3	18-33	1	1	19.6	19.6 19.6	7 4	1455	DAY	52	4.7	4.7	4.7	5.C	4.7	NONE	-	29.6 30.9 30.2
B 4	C-15	6	6	19.6	14.2 23.5	7 4	1324	DAY	62	5.3	5.5	5.4	5.5	4.8	NONE	-	32.8 33.5 33.2
B 4	18-33	3	3	21.2	18.1 25.3	7 4	1324	DAY	62	5.0	5.3	5.2	5.5	4.8	NONE	-	33.7 34.1 33.9
B 5	C-15	9	9	15.9	11.7 18.1	7 4	1156	DAY	77	4.2	4.9	4.5	4.9	3.9	NONE	-	31.0 32.5 31.6
B 5	18-33	3	3	23.6	16.7 34.5	7 4	1156	DAY	77	3.7	4.1	3.9	4.9	3.9	NONE	-	30.4 32.7 31.9
B 6	C-15	11	11	18.4	13.6 22.5	7 4	1005	DAY	87	4.4	4.7	4.6	4.7	2.8	NONE	-	32.2 33.2 32.8
B 6	18-33	12	12	16.5	10.5 20.5	7 4	1005	DAY	87	4.1	4.3	4.3	4.7	2.8	NONE	-	33.2 33.3 33.2
B 7	0-15	19	19	22.4	13.9 34.1	7 4	0801	DAY	95	3.5	3.9	3.8	3.9	3.2	NONE	-	32.4 33.4 33.1
B 7	18-33	4	4	16.3	14.4 19.5	7 4	0801	DAY	95	3.4	3.5	3.5	3.9	3.3	NONE	-	33.4 33.6 33.5
C 1	C-15	1	1	39.C	39.0 39.0	8 4	0035	NIGHT	21	4.5	5.C	4.9	5.C	3.5	NONE	-	31.7 32.4 32.2
C 2	0-15	6	6	37.8	31.5 42.3	8 4	0058	NIGHT	28	4.0	5.2	5.0	5.2	4.C	NONE	-	31.6 32.5 32.1
C 3	C-15	2	2	33.6	33.1 34.5	8 4	0156	NIGHT	33	4.2	4.5	4.8	4.9	3.5	NONE	-	30.6 31.4 30.9
C 3	18-24	4	4	31.6	29.8 34.0	8 4	0156	NIGHT	33	3.9	4.1	4.0	4.4	3.5	NONE	-	31.5 31.7 31.6
C 4	18-33	1	1	35.C	35.0 35.0	8 4	0316	NIGHT	44	4.4	4.4	4.4	5.0	4.4	NONE	-	33.4 33.9 33.7
C 5	0-15	2	2	25.5	22.5 28.4	8 4	0445	NIGHT	50	5.2	5.3	5.3	5.2	5.1	NONE	-	33.6 33.8 33.7
C 5	18-33	2	2	19.8	17.7 21.9	8 4	0445	NIGHT	50	5.0	5.1	5.1	5.2	5.1	NONE	-	33.8 34.3 34.0
C 6	C-15	1	1	19.2	19.2 19.2	8 4	0644	DAY	58	5.7	5.9	5.8	5.9	5.3	NONE	-	32.9 33.8 33.3
C 7	0-15	1	1	23.7	23.7 23.7	8 4	0851	DAY	69	5.4	5.5	5.5	5.5	5.2	NONE	-	33.5 33.7 33.6
C 8	0-15	2	2	17.5	15.3 19.6	8 4	1048	DAY	273	4.6	5.2	5.1	5.2	5.7	NONE	-	32.8 33.5 33.3
C 8	18-33	2	2	25.3	22.3 28.4	8 4	1048	DAY	273	4.4	4.5	4.5	5.2	5.7	NONE	-	33.6 34.0 33.8
D 1	C- 6	4	4	34.2	31.1 41.3	9 4	0213	NIGHT	18	5.9	6.C	5.9	6.C	5.5	NONE	-	30.8 31.6 31.2
D 2	0- 6	6	6	30.9	24.9 38.6	9 4	0125	NIGHT	19	6.0	6.1	6.1	6.1	5.3	NONE	-	31.5 32.0 31.8
D 3	C-15	4	4	31.3	28.6 34.1	9 4	0035	NIGHT	21	6.1	6.1	6.1	6.1	5.6	NONE	-	31.4 32.7 32.1
D 5	0-15	2	2	16.5	9.8 23.3	8 4	2127	NIGHT	40	5.4	6.C	5.7	6.C	5.2	NONE	-	32.0 33.1 32.6
D 6	0-15	1	1	44.1	44.1 44.1	8 4	1930	NIGHT	57	5.6	6.2	6.1	6.2	5.2	NONE	-	33.0 33.9 33.5
E 1	C- 6	20	20	36.7	21.3 45.5	13 4	0056	NIGHT	14	6.7	6.7	6.7	6.7	6.7	NONE	-	30.7 30.9 30.8
E 2	0- 6	26	26	37.5	22.2 48.2	13 4	0228	NIGHT	19	6.4	6.4	6.4	6.4	6.6	NONE	-	30.8 31.0 30.9
E 3	C-15	3	3	41.6	31.8 50.0	22 4	1912	NIGHT	22	7.4	7.6	7.5	7.5	7.4	NONE	-	31.3 31.4 31.3
E 5	18-24	1	1	24.4	24.4 24.4	22 4	1640	DAY	37	6.3	6.4	6.3	7.2	6.3	NONE	-	31.6 31.8 31.7
F 2	0- 6	4	4	29.1	25.9 31.0	14 4	1146	DAY	20	6.5	6.9	6.7	6.9	6.3	NONE	-	30.0 30.3 30.1
F 3	C-15	5	5	24.7	20.9 32.9	14 4	1243	DAY	27	6.3	6.5	6.4	6.5	6.3	NONE	-	31.1 31.4 31.2
F 4	C-15	5	5	37.3	33.7 44.0	14 4	1434	DAY	24	6.2	6.3	6.2	6.3	6.1	NONE	-	31.3 31.7 31.5
F 6	0-15	1	1	18.2	18.2 18.2	14 4	1719	DAY	52	6.2	6.3	6.3	6.3	6.2	NONE	-	32.2 32.3 32.3
F 7	18-33	2	2	31.3	27.8 34.9	14 4	1910	NIGHT	70	4.9	5.2	5.0	5.C	5.4	NONE	-	32.5 32.6 32.6
G 1	C- 6	3	3	33.8	28.5 37.9	15 4	0655	DAY	15	6.9	6.9	6.9	6.9	6.9	NONE	-	29.9 30.1 30.0
G 2	0- 6	4	4	24.4	21.1 31.6	15 4	0454	NIGHT	16	6.7	6.7	6.7	6.7	6.3	NONE	-	30.6 30.8 30.7
G 4	0-15	1	1	43.8	43.8 43.8	15 4	0204	NIGHT	38	6.0	6.1	6.1	6.C	6.1	NONE	-	32.2 32.4 32.3
G 5	0-15	1	1	44.3	44.3 44.3	15 4	0045	NIGHT	57	6.5	6.5	6.5	6.5	6.5	NONE	-	32.4 32.8 32.7
G 6	C-15	1	1	26.C	26.0 26.0	14 4	2245	NIGHT	94	5.0	5.C	5.0	5.C	5.6	NONE	-	32.0 32.3 32.1
G 6	18-33	1	1	32.6	32.6 32.6	14 4	2245	NIGHT	94	5.0	5.1	5.0	5.0	5.6	NONE	-	32.5 32.8 32.7
H 2	C-15	1	1	32.C	32.0 32.0	15 4	1452	DAY	21	8.5	8.6	8.5	8.6	8.5	NONE	-	31.4 31.9 31.7
H 3	C-15	1	1	30.4	30.4 30.4	15 4	1548	DAY	25	7.8	8.2	7.9	8.2	7.0	NONE	-	32.3 32.8 32.6
H 5	C-15	1	1	40.2	40.2 40.2	15 4	1911	NIGHT	37	6.6	6.9	6.7	6.9	6.6	NONE	-	32.3 32.4 32.4
H 6	0-15	7	7	26.1	21.4 37.5	15 4	2210	NIGHT	80	6.2	6.8	6.5	6.8	6.2	NONE	-	32.4 32.7 32.5
H 6	18-33	3	3	33.1	26.9 37.3	15 4	2210	NIGHT	80	6.2	6.2	6.2	6.8	6.2	NONE	-	32.4 32.5 32.5
H 7	0-15	23	21	29.6	22.2 41.3	15 4	2320	NIGHT	129	5.0	5.6	5.4	5.6	5.2	NONE	-	32.1 32.4 32.2
H 7	18-33	2	2	29.C	26.0 32.1	15 4	2320	NIGHT	129	5.0	5.4	5.3	5.6	5.2	NONE	-	32.4 32.6 32.5
J 3	C- 6	1	1	35.5	35.5 35.5	16 4	0825	DAY	19	8.9	8.9	8.9	8.9	8.5	NONE	-	31.8 31.8 31.8
J 6	0-15	4	4	35.6	33.2 39.5	16 4	0406	NIGHT	58	7.0	7.4	7.3	7.4	6.9	NONE	-	32.0 32.6 32.3
J 7	C-15	6	6	28.7	25.9 31.1	16 4	0212	NIGHT	92	6.7	6.8	6.7	6.8	6.4	NONE	-	32.3 32.5 32.4
J 7	18-33	8	8	28.3	24.2 35.8	16 4	0212	NIGHT	92	6.4	6.6	6.5	6.8	6.4	NONE	-	32.5 32.7 32.6
K 5	18-24	1	1	39.6	39.6 39.6	19 4	1553	NIGHT	37	7.7	7.9	7.8	8.8	7.7	NONE	-	32.7 32.8 32.8
M 4	C-15	2	2	30.6	17.1 44.2	20 4	1245	DAY	62	12.4	15.2	13.7	12.4	18.6	STRONG	13-20	30.7 32.2 31.6

APPENDIX TABLE -- CONTINUED

CRUISE STAT.	TOW DEPTH	LARVAE NUMBER TOTAL	LARVAE NUMBER MEAS.	LARVAE LENGTHS MEAN (MM TL)	LARVAE LENGTHS RANGE (MM TL)		DATE 1966 D M	TOW START TIME (EST)	LIGHT CONC.	WATER DEPTH (M)	TEMPERATURE (°C) RANGE	TEMPERATURE (°C) MEAN	TEMPERATURE (°C) SURF.	TEMPERATURE (°C) BOT.	THERMOCLINE DEGREE	THERMOCLINE DEPTH (M)	SALINITY (0/00) RANGE	SALINITY (0/00) MEAN
D66 5	(M)																	
A 1	0- 6	6	6	29.5	11.9	41.6	12 5	2002	NIGHT	19	7.8	7.8	7.8	7.8	7.8	NONE	-	32.5 32.6 32.6
A 2	0-15	1	1	15.2	15.2	15.2	12 5	2109	NIGHT	33	7.3	7.4	7.3	7.4	7.2	NONE	-	32.4 32.6 32.5
A 3	0-15	1	1	21.4	21.4	21.4	13 5	0008	NIGHT	37	7.2	7.2	7.2	7.2	6.6	NONE	-	31.9 32.4 32.3
A 3	18-33	1	1	24.7	24.7	24.7	13 5	0008	NIGHT	37	6.6	7.2	6.8	7.2	6.6	NONE	-	32.2 32.4 32.3
A 5	0-15	1	1	37.8	37.8	37.8	13 5	0325	NIGHT	62	6.3	6.3	6.3	6.3	4.6	STRONG	35-36	32.2 32.6 32.5
A 6	0-15	1	1	39.2	39.2	39.2	13 5	0534	DAY	76	6.5	6.5	6.5	6.5	4.3	WEAK	35-42	32.2 33.3 32.9
B 1	0- 5	7	7	35.7	16.7	60.5	13 5	2133	NIGHT	22	7.7	8.3	9.0	8.3	7.2	NONE	-	30.2 31.2 30.6
B 2	0-15	6	6	19.1	12.7	27.9	13 5	2038	NIGHT	34	7.1	7.7	7.5	7.7	5.0	NONE	-	31.3 31.9 31.7
B 3	0-15	3	3	19.8	18.7	21.2	13 5	1936	NIGHT	52	7.5	7.5	7.5	7.5	4.5	WEAK	17-23	31.7 32.0 31.8
B 5	0-15	1	1	30.0	30.0	30.0	13 5	1641	DAY	72	6.6	7.6	7.4	7.6	4.1	WEAK	12-15	32.6 33.3 32.9
C 1	0-15	4	4	24.3	14.7	38.7	14 5	2124	NIGHT	21	8.0	8.8	8.7	8.8	8.0	WEAK	12-14	30.9 31.8 31.3
C 2	0-15	1	1	57.6	57.4	57.8	14 5	2030	NIGHT	30	8.3	8.7	8.6	8.7	7.4	WEAK	17-20	31.1 31.7 31.5
C 5	0-15	1	1	35.2	35.2	35.2	14 5	1675	DAY	51	7.6	7.8	7.7	7.8	6.4	NONE	-	32.6 32.7 32.7
C 8	0-15	2	2	36.1	33.3	39.0	14 5	0615	DAY	400	6.8	7.3	7.1	7.3	8.3	NONE	-	33.2 33.3 33.2
C 8	18-33	1	1	23.8	23.8	23.8	14 5	0615	DAY	400	6.3	7.0	6.7	7.3	8.3	NONE	-	33.4 33.8 33.5
C 3	0-15	1	1	41.8	41.8	41.8	16 5	2058	NIGHT	26	8.7	9.2	9.0	9.2	7.7	WEAK	20-23	31.5 31.7 31.7
D 6	0-15	2	2	32.5	31.0	34.0	17 5	0155	NIGHT	54	8.0	8.1	8.0	8.1	6.8	NONE	-	30.3 30.9 30.6
E 1	0- 6	2	2	40.4	31.9	48.9	18 5	0414	DAWN	15	11.8	11.8	11.8	11.8	11.8	NONE	-	29.1 29.3 29.3
D6614	(M)				(MM TL)		1966 D M	(EST)		(M)							(M)	
A 1	0- 3	11	11	5.7	5.1	6.2	4 12	1956	NIGHT	17	7.4	7.5	7.5	7.5	8.5	NONE	-	32.9 32.9 32.9
B 1	0- 6	41	41	5.2	4.4	6.9	3 12	1937	NIGHT	20	8.3	8.4	8.4	8.3	8.5	NONE	-	31.8 31.9 31.9
B 3	0-15	1	1	5.1	5.1	5.1	3 12	2210	NIGHT	48	10.0	10.0	10.0	10.0	10.0	NONE	-	33.0 33.0 33.0

FOOD AND GROWTH PARAMETERS OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN CENTRAL COLUMBIA RIVER[1]

C. DALE BECKER[2]

ABSTRACT

Juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Hanford area of the free-flowing central Columbia River, Wash., consume almost entirely adult and larval stages of aquatic insects. Their diet is dominated by midges (Diptera: Chironomidae). By numbers, adult midges provided 64 and 58% of the diet and larval midges 17 and 18% of the diet, in 1968 and 1969, respectively. The families Hydropsychidae (Trichoptera or caddisflies), Notonectidae (Hemiptera or true bugs), and Hypogastruridae (Collembola or springtails) are of minor numerical importance with a combined utilization of 7% in 1968 and 15% in 1969.

Distinctive features of food and feeding activity of juvenile chinook salmon at Hanford are fourfold: 1) the fish utilize relatively few insect groups, predominantly Chironomidae; 2) they depend largely upon autochthonous river organisms; 3) they select prey drifting, floating, or swimming in the water; and 4) they are apparently habitat opportunists to a large extent. Analyses were made of variations in diet and numbers of insects consumed between six sampling stations distributed along a 38-km section of the river. Data are provided on feeding intensity, fish lengths, length-weight relationships, and coefficients of condition. Seasonal changes in river temperature and discharge, as well as variations in regulated flow levels, are environmental features influencing feeding, growth, and emigration of fish in the Hanford environs.

Food habits of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), have been reported from various habitats including the Sacramento River, Calif. (Rutter, 1904); lower Sacramento-San Joaquin system, Calif. (Sasaki, 1966); lower Chehalis River and upper Grays Harbor system, Wash. (Herrmann, 1970); middle Willamette River, Oreg. (Breuser, 1954); and tributaries of the central Columbia River, Wash. (Chapman and Quistorff, 1938). Initial observations on feeding bionomics of juvenile chinook salmon in the central Columbia River were conducted in 1968 (Becker, 1970a). The study was expanded in 1969. The objectives of this report are to present data based on the more extensive 1969 investigation and to discuss theoretically the influence of environmental features.

The mainstem Columbia River above Bonneville Dam has been altered during recent decades into a nearly consecutive series of artificial impoundments arising from hydroelectric development. Only one section of the main channel now survives in its natural, free-flowing condition. This section extends from Richland, Wash., some 93 km upriver to Priest Rapids Dam, where it forms the northern and northeastern boundaries of the Atomic Energy Commission's Hanford Reservation (Figure 1).

Most spawning grounds for salmonids throughout the mainstem Columbia River have now been inundated by the reservoir complex (Fulton, 1968). Maintenance of salmonid resources is due largely to providing access over otherwise impassable dams, propagating young fish in hatcheries and spawning channels,

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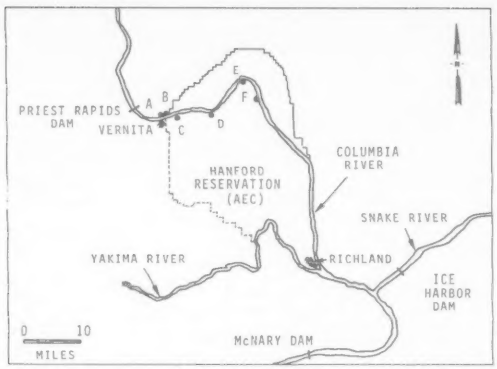

FIGURE 1.—The Hanford environs of the free-flowing Columbia River between Richland, Wash., and Priest Rapids Dam.

and protecting spawning and rearing areas in available tributaries. The free-flowing Hanford section, however, still supports a sizable spawning population of fall chinook salmon that has produced an increase from about 300 redds in 1960 to about 4,500 redds in 1969 (Watson, 1970). The annual contribution of seaward migrants from the Hanford population to the combined natural production of the Columbia and Snake Rivers is not known. But the Hanford population has clearly acquired considerable importance in sustaining natural salmonid runs within the Columbia River Basin.

ENVIRONMENTAL CONDITIONS

River temperatures and discharges are two factors potentially influencing the availability of food organisms, feeding activity, and growth of juvenile chinook salmon in the central Columbia River. The ecological aspects of these two factors are evaluated in the Discussion of this report.

The annual cycles of temperature and discharge (Figure 2) are essentially similar from year to year. Temperatures are lowest in January and February when eggs of fall chinook salmon are buried in the gravel, rise during the spring as fry emerge, and peak during August and September. From the standpoint of known thermal requirements (Brett, 1952), temperatures are well below the thermal preferendum of juvenile chinook salmon (12°-14°C) in March and April, enter the preferred range in May and June—when conditions are presumably optimum for feeding and growth, and extend into the upper zone of thermal tolerance during July and August.

Temperatures at Priest Rapids Dam (above Hanford) were somewhat lower than those

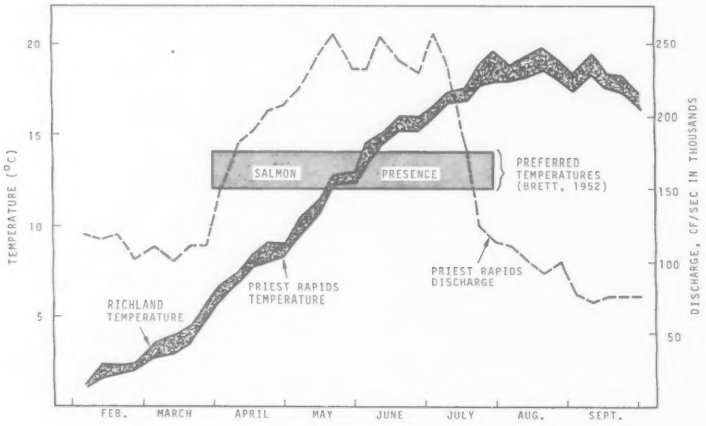

FIGURE 2.—Temperature and flow conditions in the central Columbia River during the spring and summer of 1969, in relation to the presence and preferred temperatures of juvenile fall chinook salmon.

at Richland (below Hanford) in 1969 largely because of thermal discharges from operating plutonium-production reactors on the Hanford reservation.[3] Solar radiation also contributes heat to the free-flowing river above Richland during the summer (Moore, 1968). Maximum daily temperatures recorded in 1969 at Priest Rapids Dam and Richland were 19.7° and 20.6°C, respectively. These peaks were well below the apparent upper incipient lethal level of 25.1°C for juvenile chinook salmon, experimentally determined (Brett, 1952).

The annual volume of river flow in the central Columbia River ranges from about 40,000 to over 300,000 cfs (1,133-8,500 m³/sec). Flows are low during the fall and winter, but increase and peak during April, May, and June due to the seasonal runoff of the spring freshet. In 1969, flows increased about 6 weeks earlier than normal because of operational releases at Grand Coulee Dam on the upper Columbia River. High flows were sustained for about 3 mo, then decreased sharply in July, and minimum summer flows occurred in late August and September.

The discharge data illustrated in Figure 2 are based on weekly means and fail to reveal the extent of either weekly or daily fluctuations in river levels that occur from flow regulation at Priest Rapids Dam. Flows are generally reduced on weekends and increased during the week in response to consumer demands for hydroelectric power (Figure 3). Similar but less extreme variations are induced daily. Water in excess of reservoir capacity is discharged over spillways at Priest Rapids Dam during the spring spate. Weekly fluctuations in river volumes are more variable at other seasons because greater need exists to conserve reservoir water supplies for hydroelectric production. At these times, such as in March and August 1969, flow regulation on weekends may result in changes of water level in the Hanford area of up to 2 m in 24 hr.

[3] Four reactors were discharging heated water in 1968 and the spring of 1969. The effluents issued as point discharges from subsurface locations in midriver at depths exceeding 6 m, and the mixing zones extended downstream in narrow bands prior to dispersal. Juvenile salmonids feeding in inshore areas below the reactors were not directly exposed to thermal increments.

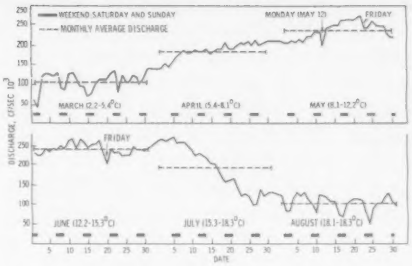

FIGURE 3.—Weekly and daily fluctuations in flow volumes in the central Columbia River due to regulation at Priest Rapids Dam, above Hanford, March-August 1969.

Juvenile fall chinook salmon occur in the Hanford area of the Columbia River from late March to mid-July (Figure 2) (Mains and Smith, 1964; Becker, 1970b). During this span the eggs hatch, fry leave the gravel of the riverbed, and juvenile fish occupy inshore feeding areas for indeterminate periods of feeding and growth before departing seaward. Most juveniles lingering at Hanford emigrate by the end of July. The short residence span is a historical characteristic of juvenile fall chinook salmon originating in the central Columbia River. However, the timing of the seaward migration of juvenile salmonids passing through the upper and lower Columbia River system is now delayed by the reservoir complex (Park, 1969; Raymond, 1969).

METHODS

Juvenile chinook salmon of the 0-age group, produced by adults spawning during the fall of 1968, were collected by seines at stations along the river banks from 4 March to 29 July 1969. The sampling span corresponded to the annual presence of fish following emergence from the gravel and preceding seaward migration. Stomach analyses of 769 fish were made from samples collected at roughly weekly intervals, when available. All samples were collected between 0900 and 1500 hr, and preserved in 10% buffered Formalin[4] immediately

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

after capture to stop digestive action. The fish were later measured (fork length, FL) and eviscerated. All measurements were taken after 7 days of preservation to obtain consistency, since Formalin causes some initial shrinkage. Organisms in the stomachs were identified individually to the lowest practical category under a dissecting microscope with the aid of appropriate taxonomic texts, classified according to their developmental stage, and enumerated. Insects represented by chitinous head capsules, particularly larval Chironomidae, were counted as complete organisms whereas fragmented body parts were excluded.

The 1968 study quantified only the food organisms consumed. Methods in 1969 were modified to provide data on fish length-weight relationships and dry weight (biomass) of the stomach contents. Fish were individually blotted with absorbent paper to remove excess fluid prior to weighing. After identification and enumeration of food organisms, the entire stomach content of each fish was placed in a miniature watch glass, air dried at least 24 hr in a controlled atmosphere, and weighed.

Collecting stations were distributed along a 38-km section of the Columbia River extending downstream from the Highway 240 bridge at Vernita, Wash. Six primary stations, shown in Figure 1 (A, B, C, D, E, F), and four supplementary stations were used. Samples from all 10 stations were combined in summations of food organisms utilized (see Tables 1 and 2), but only data from the six primary stations were used for subsequent statistical treatment.

RESULTS

Food Organisms Utilized

Throughout their sojourn at Hanford, over 95% of the diet of juvenile chinook salmon consisted of insects. The prey included adult, subadult, and larval stages of semiaquatics, various developmental stages of aquatics, and winged adults of terrestrials (Table 1). Comparison of the 1968 and 1969 data in Table 1 reveals that the organisms consumed were essentially similar in two successive years.

The Chironomidae (midges) were the dominant insect group utilized. Emerging subadults and adults were captured in abundance, 64% in 1968 and 58% in 1969. Midge larvae were taken less extensively, 17% in 1968 and 18% in 1969. Few midge pupae and no pupal exuviae were noted.

The order Diptera provided 83% and 78% of all insects utilized in 1968 and 1969, respectively. Other insect groups were of less importance in terms of numbers, but not necessarily in volume (or nutritional value) since sizes of different species vary considerably. The relatively large Trichoptera (caddisflies), consisting primarily of *Hydropsyche cockerelli* (Hydropsychidae), were numerically the second most important order. Like the midges, most caddisflies eaten were recently emerged adults associated with the water-air interface. Other groups of secondary importance were the families Notonectidae (Hemiptera or true bugs), primarily small *Notonecta* nymphs, and the Hypogastruridae (Collembola or springtails).

Few Ephemeroptera (mayflies), often important dietary items of salmonids in other streams, and no Plecoptera (stoneflies) were detected in the stomach contents. Unpublished data from limited bottom samples, sporadic drift samples, inspection of stones, and trapping of adult insects by light attraction at night indicate that populations of mayflies and particularly stoneflies are low in the central Columbia River. Zooplankton, originating primarily from the Priest Rapids reservoir and present in the river drift, were utilized in small quantities by only a few fish.

Seasonal Changes in Diet

Some change occurs in the diet of juvenile chinook salmon from March to July (Table 2). The Chironomidae accounted for the greatest proportion of food organisms each month on a numerical basis, with the most larval and adult midges being consumed in March and April. Hemiptera and Collembola, both consisting of small forms, received maximum utilization in April, May, and June when rising river volumes inundated shoreline areas. Adult Trichoptera were consumed primarily in June

TABLE 1.—Organisms consumed by juvenile chinook salmon (0-age group) in the central Columbia River. (435 fish examined in 1968 and 769 fish in 1969.)

Food organism	1968[1] Number	1968[1] %	1969 Number	1969 %
Diptera:				
Adults:				
Chironomidae[2]	5,973	63.5	11,062	58.2
Dolichopodidae	31	0.3	6	[3]0.0
Empididae	13	0.1	4	0.0
Simuliidae	4	0.0	52	0.3
Culicidae	0	—	6	0.0
Ephydridae	1	0.0	3	0.0
Heleidae	0	—	1	0.0
Stratiomyidae	0	—	1	0.0
Dixidae	0	—	1	0.0
Unidentified	82	0.9	193	1.0
Larvae:				
Chironomidae	1,596	17.0	3,450	18.1
Dolichopodidae	18	0.2	4	0.0
Empididae	0	—	1	0.0
Simuliidae	55	0.6	54	0.3
Ephydridae	1	0.0	1	0.0
Heleidae	3	0.0	0	—
Muscidae	3	0.0	0	—
Unidentified	7	0.1	9	0.0
Pupae:				
Chironomidae	7	0.1	18	0.1
Tipulidae	5	0.1	0	—
Heleidae	0	—	2	0.0
Unidentified	5	0.1	4	0.0
Total Diptera	7,804	83.0	14,872	78.3
Hemiptera:				
Notonectidae	248	2.6	918	4.8
Mesoveliidae	34	0.4	2	0.0
Macroveliidae	1	0.0	0	—
Corixidae	1	0.0	1	0.0
Saldidae	4	0.0	8	0.0
Hebridae	1	0.0	0	—
Unidentified	11	0.1	27	0.1
Total Hemiptera	300	3.2	956	5.0
Coleoptera:				
Adults:				
Unidentified	4	0.0	23	0.1
Larvae:				
Dytiscidae	26	0.3	13	0.1
Noteridae	1	0.0	0	—
Hydrophilidae	1	0.0	1	0.0
Elmidae	0	—	1	0.0
Ptilodactylidae	1	0.0	0	—
Unidentified	1	0.0	16	0.1
Total Coleoptera	34	0.4	54	0.3
Lepidoptera:				
Unidentified adults[4]	3	0.0	187	1.0
Unidentified larvae[4]	0	—	21	0.1
Total Lepidoptera	3	0.0	208	1.1
Trichoptera:				
Adults:				
Hydropsychidae	277	2.9	948	5.0
Psychomyiidae	0	—	3	0.0
Calamoceratidae	0	—	6	0.0
Hydroptilidae	0	—	12	0.1
Unidentified	93	1.0	44	0.2
Larvae:				
Hydropsychidae	18	0.2	93	0.5
Psychomiidae	13	0.1	5	0.0
Phryganeidae	1	0.0	0	—
Rhyacophilidae	0	—	2	0.0
Unidentified	13	0.1	27	0.1
Total Trichoptera	415	4.4	1,140	6.0
Ephemeroptera:				
Subimagos:				
Unidentified	8	0.1	0	—
Nymphs:				
Baetidae	1	0.0	24	0.1
Unidentified	0	—	4	0.0
Total Ephemeroptera	9	0.1	28	0.1
Hymenoptera:				
Unidentified adults	26	0.3	27	0.1
Homoptera:				
Adults:				
Aphididae	49	0.5	245	1.3
Aleyrodidae	1	0.0	0	—
Unidentified	40	0.5	28	0.1
Total Homoptera	90	1.0	273	1.4
Collembola:				
Hypogastruridae	115	1.2	974	5.1
Other insects:				
Thysanoptera	35	0.4	11	0.1
Megaloptera	1	0.0	1	0.0
Unidentified adults	0	—	98	0.5
Unidentified larvae	0	—	11	0.1
Unidentified	165	1.7	51	0.3
Total other insects	201	2.1	172	0.9
Total insects	8,997	95.7	18,704	98.4
Other food items:				
Fish larvae	0	—	18	0.1
Acari	276	2.9	169	0.9
Zooplankton	[5] 30	0.3	[5] 15	0.1
Algae	[6] 1	0.0	0	—
Arachnida	93	1.0	97	0.5
Plant seeds	5	0.1	1	0.0
Total other food items	405	4.3	300	1.6

[1] 1968 data from Becker (1970a).
[2] Primarily emerging subadults.
[3] Less than 0.05%.
[4] Primarily *Parargyractic* sp. (Pyralidae).
[5] Number of fish containing small quantities of Cladocera, Ostracoda, Copepoda, or Amphipoda.
[6] A quantity of *Anacystis*.

TABLE 2.—Monthly changes in diet of juvenile chinook salmon in 1969, all sampling stations combined.

Food organism	Consumption per month (%)				
	March	April	May	June	July
Diptera[1]	99.5	88.8	70.2	77.2	84.8
Chironomidae, adults	67.1	62.4	50.4	52.4	77.2
Chironomidae, larvae	31.8	24.6	17.4	22.8	6.3
Hemiptera[1]	—	3.2	13.2	2.6	T[2]
Coleoptera	T	T	T	T	T
Lepidoptera	—	T	T	3.3	T
Trichoptera[1]	—	T	T	10.2	13.0
Ephemeroptera	—	T	—	T	T
Homoptera	—		T	3.4	T
Hymenoptera	—	T	T	T	T
Collembola[1]	T	5.6	13.8	1.4	—
Unknowns	—	—	T	T	—
All other insects	—	T	T	1.3	T
Total insects	99.5	97.6	97.2	99.4	97.8

[1] Major insect groups utilized.
[2] "T" = "Trace," less than 1% by number in stomach contents.

and July, in association with summer emergence of the univoltine caddisfly populations. A minor group, the semiaquatic Pyralidae (Lepidoptera or moths and butterflies), were taken most heavily in June.

Some correlation of diet (Table 2) with fish size (Figure 4) was evident. Chinook salmon fry were relatively small (35-40 mm FL) and had incompletely absorbed yolk sacs when they emerged from the gravel and began feeding in March and April. Food organisms selected by fry were predominantly small forms, primarily midges but some *Notonecta* nymphs and Collembola were included. Adult Trichoptera in June and July were selected primarily by large fish (>50 mm FL) capable of capturing and swallowing these larger insects.

Use of Drift Organisms

The developmental stages of insects ingested by juvenile chinook salmon reveal that most were floating, drifting, or swimming in the water when captured. This was apparently the situation for the selection of most Chironomidae, Hydropsychidae, *Notonecta* nymphs, and Hypogastruridae, the four main insect forms utilized. Relatively few insect stages normally adhering to epibenthic substrates or living within gravel interstices were represented in the stomach contents.

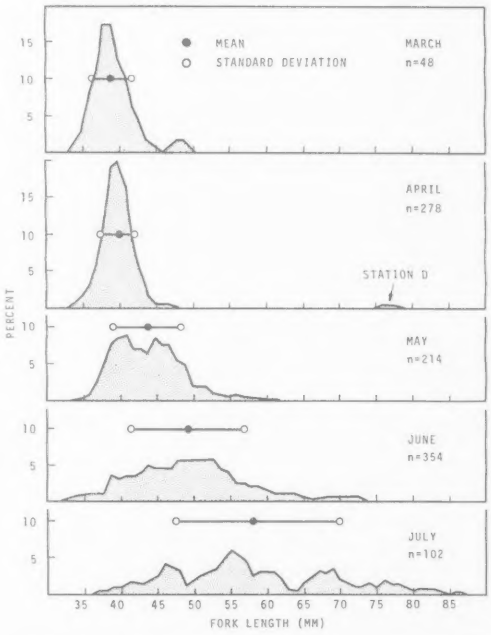

FIGURE 4.—Monthly length-frequency distributions of all juvenile chinook salmon collected at Hanford in 1969. (Data smoothed by a moving mean of three's.)

Although autochthonous insects predominated, some allochthonous terrestrial forms were ingested. The orders Homoptera, Hy-

menoptera, and Thysanoptera are almost entirely of terrestrial origin, and other true terrestrials occur among the adult Diptera, Coleoptera, and Lepidoptera, other than the Pyralidae (Table 1). The terrestrials were probably seized while drifting, either submerged or on the surface film. Since the river drift of allochthonous insects contributed less than 4% of the total food organisms by number, they were of relatively low value to the diet of juvenile chinook salmon in this study.

Variability in Diet

On a proportional basis, some differences in food occurred between the six primary stations and some intersite influences were evident (Table 3). Adult midges were highly utilized at Station D (70.1%), a shallow, semi-enclosed backwater area with somewhat warmer temperatures than other stations, but not larval midges (6.1%). *Notonecta* nymphs were captured primarily at Stations A (7.3%) and E (7.4%), both with extensive areas of marginal vegetation. Adult *Hydropsyche* were taken primarily at Stations B (9.2%) and C (7.2%), both with rubble substrates and partially exposed to flow of the main channel. Larval caddisflies were captured primarily at Station C (9.0%). Collembola were taken most extensively at Stations A (16.5%) and D (6.0%) where extensive mud-water interfaces existed. Proportional variations between stations were probably influenced by numerous intersite features including type of substrate, exposure to current flow, changes in seasonal and regulated water levels, and possibly feeding preferences of individual fish.

Although juvenile chinook salmon at all primary stations appeared to consume the same general types of food, Table 3 indicates some differences on the basis of relative proportions. To explore these differences more fully, the percentages of major food organisms in seven categories (adult and larval Chironomidae, Hemiptera, adult and larval Hydropsychidae, Collembola, and "all other insects") consumed within and between stations were retabulated on a monthly basis. Additionally, the samples were arbitrarily separated into "upper" (A, B, C) and "lower" (D, E, F) stations because of the distance separating them. Analysis by percent similarities (Whittaker and Fairbanks, 1958) was then applied with the formula:

TABLE 3.—Proportions of main insect groups utilized by juvenile chinook salmon at six primary stations, combined 1969 data.

Food organism	Relative proportion (%) at station:						
	A	B	C	D	E	F	Total
All Diptera	67.4	78.2	75.7	79.5	77.5	84.9	76.4
Chironomidae, adults	38.1	44.3	49.8	70.1	60.0	60.6	54.5
Chironomidae, larvae	26.6	31.1	24.3	6.1	15.9	21.9	19.6
Hemiptera (Notonectidae)	7.3	4.6	2.6	4.2	7.4	1.1	5.0
All Trichoptera	6.3	9.6	16.6	6.6	6.0	3.3	6.8
Hydropsychidae, adults	5.9	9.2	7.2	6.1	4.8	2.5	5.7
Hydropsychidae, larvae	0.0	0.1	9.0	0.2	0.2	0.0	0.6
Collembola (Hypogastruridae)	16.5	2.2	0.0	6.0	2.7	1.2	6.5
All adults[1]	73.0	67.3	64.4	91.5	82.7	76.1	78.4
All larvae[2]	27.0	32.7	35.6	8.5	17.3	23.9	21.6

[1] Includes all winged forms, aquatic insects as well as terrestrials, plus Hemiptera and Collembola.
[2] Includes larvae, pupae, nymphs, and other stages normally associated with benthic substrates.

$$PS_c = 100 - 0.5 \Sigma [a-b] = \Sigma \min (a, b);$$

where PS_c = percent similarity of community samples at different stations, and a and b are, for a given species (or group), the percentages of samples A and B which that species (or group) represents. This method, as adapted for food organisms, permits comparison of diets within stations being studied. It quantitatively measures the relative similarity in terms of species numerical composition, in this case, occurrence in the stomach contents of juvenile chinook.

Percent similarities for all possible monthly combinations of samples were compiled and entered in a diamond matrix (Figure 5). Values of combined samples for all upper and lower stations ranged from a low 58.5 in May, 68.8 in April, 70.4 in June, to 75.5 in July (dark areas).

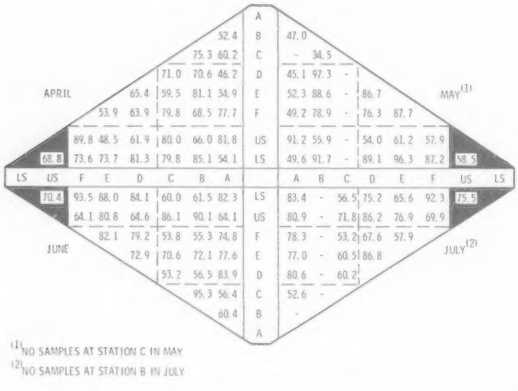

FIGURE 5.—Diamond matrix comparison of percent similarities (PS_c) between and within upper (A, B, C) and lower (D, E, F) stations based on major food organisms consumed, April-July 1969.

Monthly computed figures within and between individual stations ranged above and below these values. No consistent pattern was evident. An upper station (A, B, or C) sometimes showed a high similarity value when compared with a lower station (D, E, or F) and sometimes a low value. For example, values for Station A versus F were high in April (77.7), June (74.8), and July (78.3) but low in May (49.2). The calculations were consistent with the conclusion that, despite the general similarity in diet (PS_c above 50% in most cases), proportional variations between stations occurred randomly in response to site habitat features and the feeding activity of individual fish.

Variability in Feeding Intensity

Mean numbers of insects in the stomach contents revealed an increasing trend from March to July (Figure 6). This increase corresponded with the span when fish size and water temperature were simultaneously increasing. During March and April, when fish

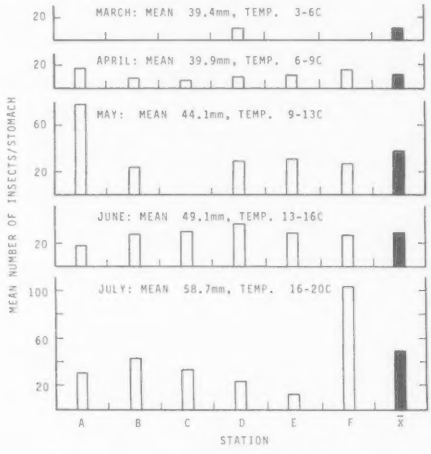

FIGURE 6.—Number of insects in stomach contents of juvenile chinook salmon at six primary stations, in relation to mean fish lengths and water temperature.

were small and temperatures were low (3°-9°C), mean numbers of insects contained were minimum, about 10 per fish. Mean numbers increased to 38 in May and decreased to 28 in June. A peak of 47 was reached in July when the fish were large and temperatures ranged from 16° to 20°C. The May samples were influenced by high utilization of Hypogastruridae at Station A on 20 May, and the July samples by adult midges at Station F on 29 July, the last time fish were available. If these samples were excluded, mean numbers of insects contained in May and July did not

differ greatly from those in June. Yet a slight increase throughout the season was evident.

High variations within and between samples, related to feeding of individual fish, preclude meaningful comparison between stations on the basis of number of insects per stomach. Number of insects contained under field situations is, at best, a rough index to nutrition and subsequent growth. There are several reasons. First, insects vary widely in size from minute midges to large caddisflies; large number of small insects in a stomach is not necessarily equivalent to a few large insects in terms of energy supplied. Second, the relative nutritional value may vary between like amounts of different kinds of food organisms. Third, stomach contents reveal only feeding at the approximate time a sample was taken and not the preceding meals responsible for growth. Fourth, digestion rates, metabolism, and energy consumption that result in growth are highly temperature dependent, particularly over the March to July range of 2° to 20°C that occurs in the central Columbia River. Fifth, changes in water levels influence current patterns, availability of food supply and, more or less, expenditure of energy required for a fish to obtain a "full meal."

Total stomach biomass provides better information on daily rations from natural river ecosystems. Feeding intensity on the basis of the relationship between fish size and stomach biomass was calculated as:

$$FI = \frac{w}{W} \times 100;$$

where FI = feeding intensity, w = dry weight of stomach contents in grams, and W = weight of juvenile chinook salmon in grams (Olmsted and Kilambi, 1971).

Amounts of food in the stomachs of individual fish varied widely. To minimize random sample variations, feeding intensities were tabulated on the basis of combined samples for each collection date at all primary stations (Table 4). The few fish taken in March were available only at Station D, where water temperatures were somewhat higher than in the main channel due to intragravel seepage of warm water from the shoreline. These fish revealed a relatively high feeding intensity compared to fish at all primary stations in April.

FI values from grouped samples generally increased as the season progressed and the river water warmed. The highest feeding intensity in June and early July reflects primarily an increase in the size of food organisms consumed, particularly by inclusion of adult Trichoptera (Table 2).

TABLE 4.—Feeding intensity (*FI*) of juvenile chinook salmon in the central Columbia River, 1969. (Samples combined by collection date.)

Date	Number of fish	Mean fish		Feeding intensity (*FI*)
		Length (mm)	Weight (g)	
March 4	19	38.7	0.59	0.32
11	10	38.9	0.60	0.83
April 8	75	39.7	0.62	0.32
15	58	39.8	0.62	0.19
24	57	40.0	0.66	0.14
29	56	40.7	0.70	0.14
May 13	50	41.6	0.82	0.37
20	50	45.1	1.15	0.48
27	50	46.4	1.24	0.17
June 3	50	47.2	1.38	0.70
10	38	48.7	1.69	0.57
16	57	53.6	2.30	0.66
24	40	54.1	2.15	0.45
July 2	30	54.6	2.27	0.60
7	10	49.8	1.64	0.50
15	20	59.7	2.97	0.68
21	10	68.1	4.25	0.38
29	10	78.1	6.36	0.40

Variability in Fish Lengths

The expanding standard deviation in Figure 4 indicates an increasing size range from month to month. Lengths of juvenile chinook were relatively uniform at each station during April and early May when recruitment to shoreline zones was initiated and temperatures were low. Variations in mean fish lengths within and between stations appeared with further growth in late May, as temperatures increased, and these variations became extreme in June and July. Statistical comparison of sample mean lengths throughout the season, by Duncan's Multiple Range Test, revealed significant differences that supported this observation.

Considerable turnover of fish presumably took place along the shore during the period of high river discharge and thereafter. The inference is

that groups of fish at each station were composed largely of transitory groups. Interstation turnover probably resulted from irregular movements of fish along the shoreline and seaward migration, in response to such factors as physiological stimuli, high river discharge, rising water temperature, and daily and weekly fluctuations in regulated water levels.

The combined mean lengths of fish collected at upper and lower stations provide a clearer picture of growth in relation to season (Figure 7). The slight curvilinear relationship reveals an increase in growth rates under warming temperature regimes in June and July.

Length-Weight Relationship

Although lengths of juvenile chinook salmon varied randomly between and within samples, the length-weight relationship for fish of equal size is a relatively consistent parameter. Furthermore, the relationship is characteristic of a given habitat and may indicate the adequacy of all synecological conditions leading to fish growth and development in that environment.

Preliminary statistical comparison of length-weight relationships by a nonlinear least-squares-fitted power function revealed no significant differences between stations. Consequently, the length-weight relationship of juvenile chinook salmon at Hanford was calculated by the standard regression equation $\text{Log } Y = \text{Log } A + b \text{ Log } X$. The regression was slightly curvilinear throughout the 40 to 80 mm size range (Figure 8). The computed values transform the equation to $\text{Log } \hat{Y} = -12.52 + 3.31 \text{ Log } X$.

Coefficients of Condition

In fisheries biology, the coefficient of condition is used primarily as an aid in determining the general physical status of fish stocks in different environments. The standard equation is:

$$K = \frac{W(10^5)}{L^3};$$

where K is the coefficient of condition, W is the weight of the fish in grams, L is the length of the fish in mm, and the factor 10^5 brings the value of K near unity.

Calculations were made on the basis of juvenile chinook salmon in 10-mm size groups from all primary stations combined (Table 5). K was lowest (1.08) for the 36-45 mm size group, i.e., the smallest fish emerging from the gravel in early spring and beginning to feed at low river temperatures. K values increased to the range of 1.3 to 1.4 for the larger size groups. Indices of FI for the

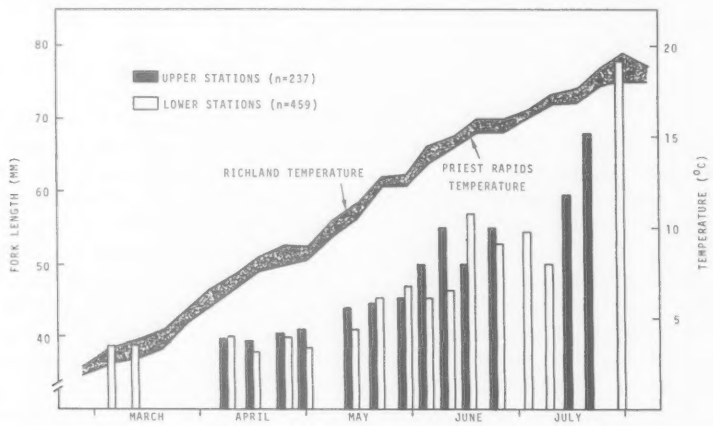

FIGURE 7.—Growth of juvenile chinook salmon at upper and lower stations, March-July 1969, in relation to Columbia River temperatures.

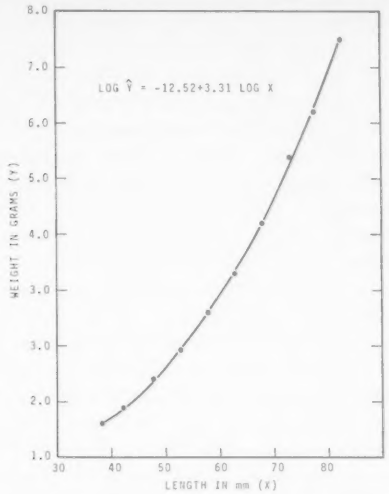

FIGURE 8.—Length-weight relationship of juvenile chinook salmon in the central Columbia River, March-July 1969.

various size groups, included in Table 5, show that the ratio of stomach food biomass to fish weight generally increases as the fish become larger. The *FI* value was low for the eight fish in the largest size group (76-85 mm) collected in late July.

DISCUSSION

Food Organisms

Distinctive features of feeding activity for juvenile chinook salmon in the central Columbia River appear to be fourfold: first, the fish utilize relatively few insect groups, predominantly Chironomidae; second, they depend largely upon autochthonous river organisms; third, they select prey drifting, floating, or swimming in the water; and fourth, they are apparently habitat opportunists to a large extent. These features are not necessarily unique among young salmonids in lotic environments. Here, in the free-flowing Columbia River, they demonstrate a close relationship with existing stream conditions.

Chironomids are of variable importance to the diet of juvenile chinook salmon in other streams. An early study conducted in the Sacramento River indicated that young chinook salmon consumed midges only to a limited extent, although floating and drifting insects did form the greatest portion of their diet (Rutter, 1904). Young chinook salmon in tributaries of the central Columbia River above Hanford in 1938 utilized few, if any, midges, although the fish fed almost exclusively on insects and the order Diptera was of greatest numerical importance (Chapman and Quistorff, 1938); these fish were relatively large, up to 152 mm, and were probably young spring chinook salmon. The food of juvenile chinook salmon in the middle Willamette River in 1958 was 39% Diptera, primarily midges, and 40% Ephemeroptera (Breuser, 1954). Emigrating chinook salmon in the lower Sacramento-San Joaquin system consumed primarily insects (90%) in 1964 but only 16% were midges (Sasaki, 1966). Adult and immature midges were a major dietary item of juvenile chinook salmon in the lower Chehalis River, along with other Diptera, Trichoptera, Plecoptera, and Ephemeroptera, in 1965 (Herrmann, 1970).

Published records reveal that insects dominate the food of other species of juvenile

TABLE 5.—Mean length, mean weight, coefficient of condition (*K*) and feeding intensity (*FI*) for 10-mm size groups of juvenile chinook salmon in the central Columbia River, March-June 1969.

Size group[1] (mm)	Number of fish	Length (mm)	Weight (g)	*K*	*FI*
36-45	411	40.5	0.72	1.08	0.33
46-55	177	50.1	1.63	1.30	0.51
56-65	57	59.1	2.76	1.34	0.55
66-75	27	70.1	4.68	1.40	0.63
76-85	8	79.0	6.53	1.33	0.25

[1] The few fish under 36 and over 85 mm in fork length were omitted.

salmonids in river habitats. However, the precise species of prey will differ between and even within various lotic systems because the existence and production of insect taxa is influenced by diverse edaphic factors.

Visual stimulation is important to the feeding of young salmonids (Chapman, 1966). Juvenile chinook salmon at Hanford exhibit considerable selection of living food organisms since nonliving material, such as insect exuviae and plant seeds, rarely occurred in their stomachs. Apparently this selection was due, in large part, to prey movement that evoked the feeding response. A preference for suspended organisms was also indicated, since benthic stages of aquatic insects were relatively unutilized by Hanford fish.

Determination of preference for a particular food organism depends on the ratios of ingredients making up the food complex and their occurrence in the stomach of fish (Allen, 1942; Ivlev, 1961). Although I obtained some invertebrate drift samples in the central Columbia River, which demonstrated an abundance of chironomid larvae, the data were inadequate for accurate determination of ratios over the entire season. Feeding apparently corresponded roughly to food organisms occurring free in the water, but not necessarily in proportion to the food actually available.

Chinook salmon fry consumed small midges most extensively whereas fingerlings tended to include larger insects in their diet. The relationship of increasing fish size to increasing food size in young salmonids has been recognized (Lindström, 1955; Hartman, 1958). Food utilized by small salmonids are subject to limitations imposed by the size of the fish whereas food utilized by larger fish can be very diverse (Mundie, 1969). However, diversity is clearly limited to what is available in a given ecosystem.

Ecological Aspects

The central Columbia River remains a large flowing river with a relatively vast water mass, rapid current velocities, and minimum shoreline habitat in relation to discharge volume. Living in stream environments requires considerable expenditure of energy that must be balanced by food consumption. Growth occurs only when energy provided by food exceeds energy expended in feeding and other activities. Energy can be conserved by juvenile salmonids in three ways: (1) leaving stream conditions to enter a lake or sea; (2) living in the stream below the main impact of the current; or (3) living predominantly in slack water, in pools, and in marginal back eddys (Mundie, 1969).

Examples of habitat selection associated with energy conservation can be noted. Young chinook salmon and steelhead trout, *Salmo gairdneri*, in Idaho streams inhabit velocities and depths in relation to body size, shifting to faster and deeper water as growth occurs (Chapman and Bjornn, 1969; Everest and Chapman, 1972). Similarly, chinook salmon fry in the Big Qualicum River, British Columbia, occupy marginal areas while the larger fish move into habitats of progressively higher velocity (Lister and Genoe, 1970). Since my samples were obtained entirely from shoreline areas that could be effectively seined, they reflect feeding in those habitats. A possible shift of larger fish to deep water would remain undetected.

Because metabolic rates of cold-blooded animals such as fish increase as temperatures rise, more food must be consumed for growth of juvenile chinook salmon to be maintained as the season advances and the water warms. My data show that feeding intensity, on the basis of both number of insects and total stomach biomass, tended to increase from March to July.

Although chironomids are small and individually low in nutritional value, they are utilized throughout the season by juvenile chinook at Hanford and their abundance compensates for a lack of size. The adult caddisflies appearing in June and July are large and provide greater nutritional value per individual at a time when temperatures are high and more energy is required for fish growth. By dry weight, 1 adult *Hydropsyche cockerelli* is equal to 35 adult midges. Although the calories available per gram of dry weight for chironomids (5,424) and hydropsychids (5,386) are nearly equal (Cummins and Wuycheck, 1971), considerably less energy is required to capture 1 prey organism than 35.

Invertebrate drift is important to the feeding of stream fish, and particularly so at Hanford. The significance of the drift phenomenon is that of increasing the availability of food and supplementing possible site limitations on insect production; moreover, under conditions of high discharge, the quantity of drift organisms passing downriver per unit of time is higher than under low flow conditions (Waters, 1969). If this is true for the central Columbia River, the annual spring spate increases the availability of food organisms to juvenile chinook salmon during their period of maximum abundance.

Changes in river water levels, both seasonal and regulated, appear to have unique significance at Hanford by exerting an influence on populations of aquatic insects and juvenile chinook salmon in inshore areas. The influence is apparent in at least four theoretical ways.

First, the annual increase in river discharge in April and May (Figure 2) inundates barren shoreline areas that are exposed to air during the preceding winter. Recolonization of flooded inshore areas by aquatic insects depends upon larvae in the drift, which may occur rapidly, or upon the deposition of eggs by adults. There are no available data on recolonization rates of recently inundated areas at Hanford. But detached insect larvae usually spend only a short time in the drift and re-attach as soon as possible (Elliott, 1967).

Second, weekly and daily variations in water level resulting from flow regulation at Priest Rapids Dam (Figure 3), which periodically floods and exposes vast stretches of shoreline areas, restricts insect recolonization and incorporates marginal dwellers into the river drift. On this basis, it is not surprising that the diet of juvenile chinook salmon includes food organisms that normally live along the shoreline such as *Notonecta* nymphs, adult springtails, and terrestrial Arachnida (spiders).

Third, station occupation by juvenile chinook salmon appears to be temporally limited. Young salmonids commonly occupy relatively small home areas (ecological niches) for a period of feeding and growth prior to seaward migration (Chapman, 1966; Edmondson, Everest, and Chapman, 1968; Chapman and Bjornn, 1969). Analysis of data from fish collected at the primary stations reveals considerable variation in sizes from week to week after mid-May. At least part of this variation must result from weekly changes in regulated water level at Priest Rapids Dam (up to 2 m in 24 hr on weekends) that implements population turnover.

Fourth, the eminent decline in river discharge volume from the annual spring spate ($>300{,}000$ cfs) to the summer period of low flow($\simeq 40{,}000$ cfs) suggests that the falling water level is one factor involved in prompting seaward juvenile chinook salmon still lingering at Hanford. At any rate, the seasonal increase and then decrease in river flows accompanied by rising temperatures (Figure 2) are the main environmental factors correlated with seaward migration. These phenomena, which have occurred annually throughout recorded history, may well have played an evolutionary role in the development of the spring migration characteristic for young fall chinook salmon produced in the Columbia River ecosystem.

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LITERATURE CITED

ALLEN, K. R.
1942. Comparison of bottom faunas as sources of available fish food. Trans. Am. Fish. Soc. 71: 275-283.

BECKER, C. D.
1970a. Feeding bionomics of juvenile chinook salmon in the central Columbia River. Northwest Sci. 44:75-81.
1970b. Temperature, timing and seaward migration of juvenile chinook salmon from the central Columbia River. U.S. AEC, Res. Dev. Rep. (BNWL-1472), Battelle Northwest, Richland, Wash., 21 p.

BRETT, J. R.
1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9:265-323.

BREUSER, R.
1954. Food and growth of juvenile coho salmon *Oncorhynchus kisutch* (Walbaum) and chinook salmon *Oncorhynchus tshawytscha* (Walbaum) in certain Oregon streams. MS Thesis, Oregon State Univ., Corvallis.

CHAPMAN, D. W.
1966. Food and space as regulators of salmonid populations in streams. Am. Nat. 100:345-357.

CHAPMAN, D. W., AND T. C. BJORNN.
1969. Distribution of salmonids in streams with special reference to food and feeding. *In* T. G. Northcote (editor), Symposium on Salmon and Trout in Streams, p. 153-176. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. B. C., Vancouver.

CHAPMAN, W. M., AND E. QUISTORFF.
1938. The food of certain fishes of north central Columbia River drainage, in particular, young chinook salmon and steelhead trout. Wash. State Dep. Fish., Biol. Rep. 37A, 14 p.

CUMMINS, K. W., AND J. C. WUYCHECK.
1971. Caloric equivalents for investigations in ecological energetics. Int. Ver. Theor. Angew. Limnol. Verh. 18, 158 p.

EDMUNDSON, E., F. E. EVEREST, AND D. W. CHAPMAN.
1968. Permanence of station in juvenile chinook salmon and steelhead trout. J. Fish. Res. Board Can. 25:1453-1464.

ELLIOTT, J. M.
1967. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol., New Ser. 63:202-237.

EVEREST, F. H., AND D. W. CHAPMAN.
1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. 29: 91-100.

FULTON, L. A.
1968. Spawning areas and abundance of chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin—past. and present. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 571, 26 p.

HARTMAN, G. F.
1958. Mouth size and food size in young rainbow trout, *Salmo gairdneri*. Copeia 1958:233-234.

HERRMANN, R. B.
1970. Food of juvenile chinook and chum salmon in the lower Chehalis River and Upper Grays Harbor. *In* Grays Harbor Cooperative Water Quality Study 1964-1966, p. 59-82. Wash. State Dep. Fish., Tech. Rep. 7.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. (Translated from the Russian by D. Scott.) Yale Univ. Press, New Haven, 302 p.

LINSTRÖM, T.
1955. On the relation of fish size—food size. Rep. Inst. Freshwater Res., Drottningholm 36:133-147.

LISTER, D. B., AND H. S. GENOE.
1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. 27:1215-1224.

MAINS, E. M., AND J. M. SMITH.
1964. The distribution, size, time and current preferences of seaward migrant chinook salmon in the Columbia and Snake Rivers. Wash. Dep. Fish., Fish. Res. Pap. 2(3):5-43.

MOORE, A. M.
1968. Water temperatures in the Columbia River Basin July 1966 to September 1967. Open File Report, U.S. Geological Survey, Northwest Water Resources Data Center, Portland, Oreg., 39 p.

MUNDIE, J. R.
1969. Ecological implications of the diet of juvenile coho in streams. *In* T. G. Northcote (editor), Symposium on Salmon and Trout in Streams, p. 135-152. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. B. C., Vancouver.

OLMSTED, L. L., AND R. V. KILAMBI.
1971. Interrelationships between environmental factors and feeding biology of white bass of Beaver Reservoir, Arkansas. *In* G. H. Hall (editor), Reservoir fisheries and limnology, p. 397-409. Am. Fish. Soc., Spec. Publ. 8.

PARK, D. L.
1969. Seasonal changes in downstream migration of age-group 0 chinook salmon in the upper Columbia River. Trans. Am. Fish. Soc. 98:315-317.

RAYMOND, H. L.
1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the Columbia River. Trans. Am. Fish Soc. 98:513-514.

RUTTER, C.
1904. Natural history of the quinnat salmon. A report on investigations in the Sacramento River, 1896-1901. Bull. U.S. Fish Comm. 22:65-141.

SASAKI, S.
1966. Distribution and food habits of king salmon *Oncorhynchus tshawytscha*, and steelhead rainbow trout, *Salmo gairdnerii*, in the Sacramento-San Joaquin Delta. *In* Ecological studies of the Sacramento-San Joaquin Delta, Part II. Fishes of the Delta, p. 108-114. Calif. Dep. Fish Game, Fish Bull. 136.

WATERS, T. F.
1969. Invertebrate drift - ecology and significance to stream fishes. *In* T. G. Northcote (editor), Symposium on Salmon and Trout in Streams, p. 121-134. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. B. C., Vancouver.

WATSON, D. G.
1970. Fall chinook salmon spawning in the Columbia River near Hanford 1947-1969. U.S. AEC, Res. Dev. Rep. (BNWL-1515), Battelle Northwest, Richland, Wash., 40 p.

WHITTAKER, R. H., AND C. W. FAIRBANKS.
1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39:46-65.

SOME ASPECTS OF THE ECOLOGY OF LANTERNFISHES (MYCTOPHIDAE) IN THE PACIFIC OCEAN NEAR HAWAII

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ABSTRACT

Most species of myctophids collected near Hawaii showed ontogenetic differences in vertical distribution and migration. Newly transformed juveniles of several species did not regularly migrate. Within both day and night depth ranges, the smaller fish tended to occur shallower than the adults. Few differences were related to sex or reproductive condition. Large fractions of populations of three species appeared not to migrate at certain seasons. Seasonal changes in size composition of populations and ripeness of mature females indicated that most abundant species spawn principally in the spring and summer and live about 1 year. The size-depth patterns of congeners and closely related species were quite different, while similar-sized individuals of dissimilar species tended to co-occur at the same depths.

Comparison of day and night estimates of abundance and size composition indicated that there was little differential avoidance by most species. There were differences between catches by a 10-ft Isaacs-Kidd trawl and a modified Cobb pelagic trawl related to both species and size with neither trawl showing a distinct advantage for all species. Comparison of catches at full and new moon indicated that at full moon most species occurred about 50 m deeper and avoided the Isaacs-Kidd trawl better than at new moon.

The average standing crop of myctophids was about 0.32 g(wet weight)/m^2, and the yearly turnover rate was estimated at roughly twice the standing crop. Myctophids and other vertically migrating micronekton appear to be very important in the trophic structure of the tropical open ocean and probably account for most of the consumption of zooplankton.

Myctophids or lanternfishes are one of the dominant families of mesopelagic fishes and are generally thought to be important in the open ocean ecosystem because of their frequent occurrence and apparently great abundances. The bulk of early work was concerned primarily with taxonomy and distribution. Most recent work has concentrated on one aspect of their ecology, diurnal vertical migration. Myctophids have been shown in a number of cases, e.g., Paxton (1967), Badcock (1970), to undertake substantial migrations from depths of several hundred meters during the day to the upper 100-200 m at night, but few studies have done more than describe the vertical distribution patterns and suggest possible relationships of these to gradients in temperature or light with depth or with the position of sonic scattering layers. There are numerous gaps in our knowledge of other aspects of the ecology of this ubiquitous group of fishes. Moreover, previous work has not been equitably distributed in a geographic sense; most has been carried out at higher latitudes.

Among others, Badcock (1970) has indicated that there are size-specific differences in migration patterns of some species of myctophids, but ontogenetic changes in depth distribution have not been studied quantitatively. Similarly, Nafpaktitis (1968) has indicated that in some species of the genus *Diaphus* the mature females do not migrate. It is not known whether either of these patterns is typical or widespread within the family. Extensive life history data have been presented for some abundant northern species, *Benthosoma glaciale* (Halliday, 1970), *Stenobranchus leucopsaurus* (Smoker and Pearcy, 1970), and *Myctophum affine* (Odate, 1966), but the life histories of most species, particularly tropical ones, remain unknown.

This paper presents and discusses data on myctophids collected in several series of mid-

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water trawl samples taken in the Central Pacific Ocean near Hawaii. The majority of the samples were collected during four series which attempted to cover the upper 1,000 m day and night at 3-mo intervals over a period of 1 year. The aims of the sampling were to determine the vertical migration patterns of the species present and to examine changes in abundance, size composition, and reproductive state with depth and season. In addition, changes in vertical distribution and avoidance with changing phases of the moon were investigated, and the catching ability of a 10-ft Isaacs-Kidd mid-water trawl was compared with that of a much larger anchovy trawl. The results allow detailed description of many aspects of the life history and ecology of myctophids. It is possible from these data to consider interspecific relationships with respect to time and space and to estimate the importance of myctophids and other micronekton in the tropical, open ocean ecosystem.

MATERIALS AND METHODS

A total of 221 mid-water trawl samples were taken for this study. Fifty-four were taken with a 6-ft Isaacs-Kidd (IK) mid-water trawl, 157 with a 10-ft IK trawl, and 10 with a modified Cobb pelagic trawl (CT). All trawls were fished without opening-closing devices. Thirty-seven IK tows were taken during September and November 1969 to provide preliminary data. The remaining tows consisted of four general types: a series of 31 6-ft IK tows taken in July 1970 to check various aspects of sampling, four series of 26-35 10-ft IK tows each taken at 3-mo intervals from September 1970 to June 1971, 17 10-ft IK tows taken in September and October 1971 to determine effects of moon phase on sampling, and 10 CT tows taken in conjunction with the 10-ft IK tows during February-March 1971.

All tows except those of November 1969 were taken west of the island of Oahu, Hawaii, roughly along a line between lat. 21°20′N; long. 158°20′W and lat. 21°35′N; long. 158°35′W. The depth of water for all tows was 1,800 m (1,000 fm) or more. BT casts to 300 m made during the study indicated that seasonal temperature changes in the study area were nearly the same as for a nearby station (lat. 22°10′N; long. 158°W) studied more thoroughly by Gordon (1971). Presumably the depth profiles of other physical-chemical factors given by Gordon (1970, 1971) are also representative of the study area. The November 1969 tows were taken near Gordon's station.

The IK trawls were of standard dimensions and were lined with 6.35 mm (¼ inch) knotless nylon mesh anteriorly and 4.75 mm (3/16 inch) knotless nylon mesh posteriorly. The 10-ft IK terminated with a 1.0-m diameter plankton net of 333 μ nitex; the 6-ft, with a 0.5-m diameter net. The CT, described in detail by Higgins (1970), had 19-mm stretch mesh in the main body and a cod end lined with 6.35-mm mesh. Diver observations of the CT have indicated that the mouth opening under tow is about 12 m wide by 8 m high (Higgins, 1970).

IK trawls were fished from the University of Hawaii RV *Teritu*. Unless otherwise noted, the procedure was the same for all tows. The trawl was shot with the ship moving about 1.75 m/sec (ca. 3.5 knots), and the cable was paid out so that just enough tension was maintained to keep the net from fouling. For deeper (over 300 m) tows, the ship was slowed to ca. 1.0 m/sec for a few minutes after the cable was paid out to allow the trawl to sink farther. These procedures were designed to minimize forward motion while the trawl descended to towing depth. The trawl was towed at depth for 2-3 hr at a speed of about 1.75 m/sec. For retrieval, the ship was slowed to ca. 1.0 m/sec, again to minimize forward motion while the trawl was above sampling depth. Cable was retrieved as fast as possible; the average rate varied between 30 and 60 m/min. The rate was considerably faster than 60 m/min when there was more than 1,000 m of wire out. The CT was fished in a similar manner from the National Marine Fisheries Service (NMFS) RV *Townsend Cromwell*.

Depth of tow was determined by time-depth recorders (Benthos, Inc.)[2] attached to the trawl. For depths of less than 300 m the trawl reached

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

towing depth within a few minutes after cable was paid out and usually stayed within 5 m of this depth during the entire tow. For deeper tows, the trawl frequently took some time to descend to maximum depth and often moved up and/or down gradually during the tow. In all cases, however, a single, most frequently fished depth was assigned to each tow.

For some IK tows an acoustic telemeter (Benthos, Inc.) was used to determine depth while underway and to reach desired depth, but in most cases the amount of cable required to reach a given depth had to be estimated beforehand. This method required some practice, and, needless to say, depth coverage was more even for the later cruises.

Towing speed for the IK was, in some cases, measured by a TSK flowmeter attached to the trawl and rigged to signal, through the telemeter, every 500 revolutions. In all cases, position of the ship was determined by visual or radar fixes at ½- to 1-hr intervals during the tow and speed calculated from these data. The towing speed for the IK varied between 1.54 and 1.98 m/sec with most tows about 1.75 m/sec. The CT was towed at about 1.5 m/sec.

Assuming 100% filtering efficiency and a speed of 1.75 m/sec, the 10-ft IK sampled about 9.4×10^4 m^3 per 2-hr tow. At 1.5 m/sec, the CT sampled just over 10^6 m^3 per 2-hr tow or about 11 times the IK tows. Only fish over 10-mm long were considered sampled quantitatively by the IK since smaller individuals could pass through the meshes. Larger fish, up to 25-30 mm long, appeared to escape through the CT meshes.

The July 1970 (5-10 July 1970) series of tows with the 6-ft IK were designed primarily to determine whether significant changes in vertical distribution occurred in the upper layers during the course of night and to obtain an estimate of sample variability. At depths of 50 m and 100 m, five 2-hr tows were taken from dusk to dawn on a single night, and one replicate tow was made during the following night. Dusk, dawn, and night tows were taken at other depths in the upper 400 m. In addition, day tows were taken between 500 and 1,125 m.

The four quarterly series of 10-ft IK tows were designed to sample for seasonal changes and were intended to be replicate surveys of the upper 1,000 m both day and night. Since preliminary day tows caught no nonlarval myctophids above 300 m, no attempt was made to cover the upper layers during the day. The dates of the cruises were 14-17 and 20-24 September 1970; 8-10 and 13-17 December 1970; 26 February-3 March and 19 March 1971; and 8-11 and 15-19 June 1971. The series will subsequently be called September 1970, December 1970, March 1971, and June 1971. Depths sampled for these series and the July 1970 series are given in Figure 1.

In addition to some gaps in depth coverage during September 1970, the shallow night tows were made at both full and new moon. Subsequent analyses showed that the depth distribution and avoidance for many species changed considerably with moon phase, and as a consequence, some populations were sampled

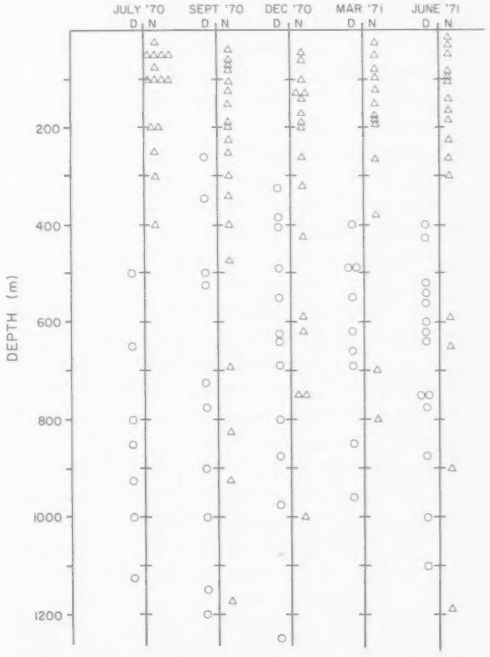

FIGURE 1.—Depths of Isaacs-Kidd trawl samples taken during July 1970, September 1970, December 1970, March 1971, and June 1971. Day samples are designated by circles, night samples by triangles.

twice and others not at all during the September 1970 series. This also occurred to a lesser extent during the December 1970 series. All night tows above 200 m were made during new moon for the March 1971 and June 1971 series. The March 1971 series was incomplete due to a storm, and the 400-700 m zone was not sampled at night. Such limitations are taken into account in interpreting the data.

The CT tows were taken in conjunction with the March 1971 IK series. Eight night tows were taken at 25-m intervals between 25 and 200 m during the same three nights that IK tows were taken at or near these depths. The IK-CT pairs were unfortunately not all taken simultaneously. All tows but one were 2 hr at depth; the 25-m CT tow was only 15 min long, but catches of some species were sufficient for useful analyses. Two day tows at 300 and 400 m were also taken with the CT during this period.

To determine effects of moon phase on vertical distribution and avoidance at night, 10-ft IK tows of 1½ hr each were made at depths of 15, 45, 65, 80, 100, 125, 145, and 165 m on 17-19 September 1971 (new moon) and at 20, 50, 75, 100, 130, 170, and 190 m on 4-6 October 1971 (full moon). This series, designated September 1971, also provided useful data on other aspects.

During December 1970 and June 1971, three and four, respectively, short oblique tows were made to depths of 250-300 m at night in order to roughly estimate the catch due to ascent and descent through the upper layers. The cable was paid out as described above, but the ship was slowed and the trawl retrieved immediately. A longer oblique tow was made in June 1971 to 330 m at night. Fifty meters of cable was paid out every 15 min in an attempt to sample all depths equally.

The dusk and dawn tows taken during July 1970 indicated that myctophids had completed their upward migration by 2000 hr and had begun to descend by 0400-0500 hr. All subsequent night tows were taken between these times. Differences between tows taken in sequence at 50 and 100 m through the night were not markedly greater than differences between tows taken at the same hour on two successive nights. There was no trend among the species which indicated that anything analogous to a "mid-night dispersal" occurred. Therefore, all night tows were considered together regardless of what period of the night they were taken. No comparable study was made to check on possible changes in depth distribution during the day. It was assumed that no changes took place during the day between 0800 and 1600 hr.

Specimens were preserved in Formalin. Standard length was measured to the nearest mm for all collected by IK. For some CT collections of over 1,000 individuals per species, a subsample of several hundred was measured. Wet weights of blotted specimens were determined to the nearest mg for small individuals and to the nearest 10 mg for larger fish or whole samples.

Insufficient replicate samples were taken to reliably specify the variance associated with the estimate of abundance from a single tow. There was considerable variability in the catches of the two series of four tows each taken at 50 and 100 m in July 1970. (Appendix Table 1.) In particular, one tow in the 100 m series caught much higher numbers of several species. This variability, probably related to patchiness in the organisms sampled and differences in avoidance due to differences in ship's speed, cloud cover (light), etc., limits interpretation of some of the data. Where I have drawn conclusions without statements of statistical significance, I have attempted to be conservative. Features not consistently evident from a series of tows should be regarded as tentative.

The significance of differences between two samples in size composition was determined using the Kolmogorov-Smirnov test (Tate and Clelland, 1957). Two samples were considered significantly different if the probability (one-tailed) associated with the maximum difference between the cumulative size-frequency curves was less than 0.05. The overall significance of the differences is somewhat altered because multiple tests were often made with the same data. In most cases, the trends observed were obvious and consistent, and it is doubtful that large errors resulted from the procedure.

There were relatively few significant differences in size composition between replicates at the same depth. For 10 sets of data for eight

species caught in abundance in the replicates at 50 and 100 m during July 1970, there were no significant differences between size-frequency curves in seven and only one sample in each of the other three sets differed significantly from one or more of the other replicates.

Not all individuals were sexed and no detailed gonad studies were done. Size at maturity was taken as the minimum size at which females were found with obviously ripened ova. A variable number of each species were examined. For abundant species, sex was determined for about 50 juveniles, and sex ratio of mature fish and ripeness of mature females were determined for samples from several depths and seasons. If significant or nearly significant differences between samples were noted, a larger series was examined to determine trends. It was assumed that the percentage of females among mature fish and the percentage of ripe out of total mature females were distributed as a binomial and that the differences in percentages were considered significant if the 95% confidence limits did not cross zero.

For species collected in low numbers, the data from each series were simply pooled to estimate overall size composition and relative abundances. For abundant species, total numbers and overall size composition for the entire water column were computed by a rectangular integration of the depth-abundance curves. Numbers collected were adjusted to a 2-hr towing time. It was assumed that abundance and size composition from the depth sampled were the same for the layer between the midpoints between that depth and the next shallower and next deeper depth sampled; i.e., abundance estimated from a sample at depth z_i was assumed constant throughout $(z_{i-1} + z_i)/2$ to $(z_i + z_{i+1})/2$ where z_{i-1} was the next shallower depth sampled and z_{i+1} the next deeper. The number of individuals of each size in each sample was weighted accordingly.

Differences in the numbers and size composition of these calculated totals could not be compared statistically since no estimate of the variances of the data were available, but where depth coverage was adequate, calculated totals and size-frequency curves were used to roughly compare whole series for day and night, seasonal, full and new moon, and IK and CT differences. The calculated size-frequency curves for December 1970 and June 1971 could be compared with those of the oblique tows when sufficient specimens of a given species were taken in the latter. Unless there were obvious deficiencies in depth coverage, etc., the calculated curves agreed closely with those from the oblique tows.

RESULTS

A total of 47 species of myctophids were collected. The number collected, size range, size at maturity for females, and day and night depth ranges are given in Table 1. Unless noted under individual species headings (below), the individuals caught did not deviate from species descriptions in Wisner (1971, manuscr.[3]), Nafpaktitis (1968), or Nafpaktitis and Nafpaktitis (1969).[4] The percentage of ripe females among total mature females examined for each of the four quarterly cruises is given for several abundant species in Table 2.

The depth ranges given in Table 1 are the best estimates based on all available data. Because the trawl was open during descent and ascent, some individuals were caught in tows made below the levels where they occurred. For abundant species, catches below the depth ranges given were low and consistently close to those of short oblique tows (see Appendix Table 2). A few cases where substantial numbers were caught near the day depth at night are discussed below under the species headings. For rarer species, where the chances of being caught in a tow at their actual depth were not much greater than the chances of being caught in transit by deeper tows, catches due to contamination could not be readily distinguished and the lower depth limits in Table 1 may be erroneous. In most cases, the values given are conservative.

[3] Wisner, R. L. Unpubl. manuscr. Annotated and illustrated key to the identification of fishes of the family Myctophidae of the eastern Pacific Ocean, eastward of 160° West Longitude.

[4] Specimens of most species will be deposited at the U.S. National Museum, Los Angeles County Museum, Scripps Institution of Oceanography, and the Bernice P. Bishop Museum in Honolulu.

TABLE 1.—List of myctophid species collected, the number collected, size range, size at maturity, night and day depth ranges, and seasons when juveniles were present or present in markedly higher abundances. Under "Number collected" the figures given are the totals from the four quarterly series of samples; where few or none were caught in these series, the total number caught in all other samples is given in parentheses. Figures in parentheses under "Size range" are for dipnetted specimens.

Species	Number collected		Size range (mm)		Size at maturity (mm)	Night depth (m)	Day depth (m)	Juveniles
Protomyctophum beckeri	0	(3)	34-38		—	400 ?	400 ?	—
Benthosema suborbitale	1,157		9-38		25	15-75	490-620	June (Mar.)
Benthosema fibulatum	14	(30)	10-72		—	15-165	500-550	—
Diogenichthys atlanticus	27		12-22		17	15-100	400-600	—
Hygophum proximum	696		12-51		38	25-150	500-700	June, July
Hygophum reinhardti	413		12-48		33	50-175	550-900	all ?
Myctophum nitidulum	18	(34)	13-54	(65)	57	0-15?	600-800	—
Myctophum obtusirostrum	15	(59)	12-63	(77)	58	0-15?	500-700	—
Myctophum spinosum	5	(32)	34-93	(115)	110 ?	0-15?	600 ?	—
Myctophum selenoides	14	(24)	9-67		62	25-150	300-500	Mar., June
Symbolophorus evermanni	186		15-86		70	0-125	600-900	—
Loweina laurae	2	(3)	22-43		—	250 ?	690 ?	—
Loweina terminata	1		22		—	—	825	—
Centrobranchus choerocephalus	22		12-37		29	0-150	490-650	—
Centrobranchus andreae	4	(6)	14-47		—	100-165	640-650	—
Lobianchia gemellari	177		9-59		41	25-360	410-560	June, July, Sept.
Lobianchia urolampa	1	(1)	25-26		—	100 ?	—	—
Diaphus bertelseni	6	(79)	17-38		—	100-150	300 ?	—
Diaphus "glandulifer"	37		12-73		55	95-225	425-600	—
Diaphus schmidti	823		9-47		31	15-80	490-625	June, July, Sept.
Diaphus fragilis	56		10-83		61	15-120	520-600	Sept.
Diaphus rolfbolini	104		9-76		65	50-200	490-690	June, July, Sept.
Diaphus elucens	132		7-65		48	15-100	490-600	Sept.
Diaphus adenomus	7		71-126		—	—	495-550	—
Diaphus chrysorhynchus	7	(27)	11-84		—	75-125	550	—
Diaphus metopoclampus	1		49		—	185	—	—
Diaphus theta	0	(1)	23		—	145	—	—
Diaphus sp. A	253		9-36		25	25-85	490-525	July, Sept.
Diaphus sp. B	165		9-64		42	30-190	490-560	June
Diaphus anderseni	261		10-29		20	95-260	300-560?	June, July, Sept., Dec.
Diaphus brachycephalus	100		9-61		28	30-200	300-600?	June, July, Sept.
Notolychnus valdiviae	1,267		9-25		20	80-150	525-640	Sept. (Mar., June)
Lampadena luminosa	77		15-77		—	75-250	525-725	June, July, Sept.
Lampadena urophaos	44		17-115		100 ?	95-140	620-775	—
Lampadena anomala	1	(2)	30-49		—	300-400	800	—
Taaningichthys bathyphilus	55		20-72		51	590-930	620-800	—
Taaningichthys minimum	71		20-64		53	150-475	640-775	Mar.
Taaningichthys paurolychnus	2		20-22		—	1,175	1,000	—
Lampanyctus niger	1,946		12-135		60	100-310	640-900	Dec. (Sept.)
Lampanyctus nobilis	384		15-114		98	40-140	590-1,200	all ?
Lampanyctus steinbecki	2,362		14-56		43	80-275	625-1,000	July, Sept.
Lampanyctus tenuiformis	14		28-136		125	250-300	640-775	—
Triphoturus nigrescens	2,120		9-38		30	25-75	540-775	June, July
Bolinichthys longipes	1,458		11-56		37	50-150	525-725	June, July, Sept.
Bolinichthus supralateralis	85		12-90		88 ?	95-225	490-690	Sept., Dec.
Ceratoscopelus warmingi	3,911		11-79		45	15-140	620-1,000	Mar., June, July
Notoscopelus caudispinosus	6	(17)	20-125		111 ?	75-125	590-680	—

Eight species—*Protomyctophum beckeri, Loweina laurae, L. terminata, Centrobranchus andreae, Diaphus metopoclampus, D. theta, Lampadena anomala,* and *Taaningichthys paurolychnus*—were taken so rarely that little other than their capture in the area can be noted. For 39 species, the individual accounts below include where possible the following aspects: deviations from depth ranges given in Table 1; changes in size composition and sex ratio with depth; differential avoidance between day and night, IK and CT, and full and new moon; and changes in size composition, abundance, and reproductive state with season.

TABLE 2.—Proportion of females with developed ova among total mature females (figures in parentheses) examined for 10 species from September 1970 and 1971, December 1970, March 1971, and June 1971 samples. Significant differences between values are noted in text.

Species	September		December		March		June	
Benthosema suborbitale	0.39	(18)	0.98	(62)	1.00	(38)	—	(0)
Hygophum proximum	.78	(37)	.72	(7)	0.91	(22)	0.86	(22)
Diaphus schmidti	.375	(8)	—	(0)	.88	(59)	1.00	(11)
Diaphus sp. A	.96	(46)	1.00	(8)	.89	(9)	1.00	(14)
Notolychnus valdiviae	.70	(54)	.71	(69)	.91	(11)	.89	(38)
Lampanyctus niger	.35	(51)	.76	(95)	.88	(69)	.53	(47)
Lampanyctus steinbecki	.64	(42)	.44	(22)	.81	(103)	.78	(122)
Triphoturus nigrescens	.54	(13)	.39	(142)	1.00	(41)	.94	(36)
Bolinichthys longipes	.67	(12)	.12	(17)	.81	(70)	.88	(17)
Ceratoscopelus warmingi	.60	(102)	.62	(124)	.52	(48)	.70	(27)

Differences in sex ratio with size and season are of somewhat dubious significance and will be treated in the discussion.

Benthosema suborbitale

Small (10-12 mm) *B. suborbitale* tended to remain at depth both day and night. On all three cruises where night samples were taken near the day depth, low but probably significant numbers of small fish were taken. In June 1971, the number caught at about 550 m was nearly equal to that caught at 25 m at night and at the same depth during the day. In all cases except the June 1971 series the size-frequency curves of the deep night catches differed significantly from those of most other tows, the differences being due to much greater proportions of 10- to 12-mm fish in the deep night tows. There was no evidence that larger fish did not migrate regularly.

The depth ranges for this species were rather narrow relative to the sample spacing, and populations at a given time were usually made up of one size class. There were, however, significant differences between the size-frequency curve at 25 m and those at 50 and 80 m in March 1971. The difference was due to the absence of fish <25 mm at 50 and 80 m rather than a decrease of larger fish at 25 m. Other night series also showed a trend for smaller fish to occur higher in the water column.

There was no indication of differential day-night avoidance. The calculated size-frequency curves for day and night samples from each series agreed quite well with each other, except for June 1971. The total calculated numbers agreed well in June 1971, but for the other series, the day totals were 1.5–2× higher than the night totals. This difference was probably a result of the weighting factors assigned to the day tows being too large, i.e., the depth range was probably narrower than the relatively wide-spaced samples indicated.

The IK appears to sample *B. suborbitale* as well or better than the CT. The calculated total for the CT series was 7× that for the IK; factors for individual pairs varied between 4.2 and 8.8×. There were no significant differences between size-frequency curves of IK-CT pairs at the same depths, and the calculated curves for the two series agreed well. The fact that the CT size-frequency curves did not differ from those of the IK suggests that the lower CT estimates of abundance were not due to escapement through the meshes. If the latter had been substantial, the smaller fish would have escaped more frequently, and size composition of the catches would have differed from those of the IK.

At new moon, *B. suborbitale* occurred mostly above 50 m at night; at full moon the population was centered at about 75 m with practically none above 50 m (Figure 2). The size-frequency curves of both the individual samples and those calculated from the new and full moon series agreed closely. The numbers at peak depths were similar, and the calculated total for new moon was only 1.25× that for full moon. Thus the change in depth distribution apparent in the full moon samples was mainly if not totally due to a depression of the night depth by about 50 m.

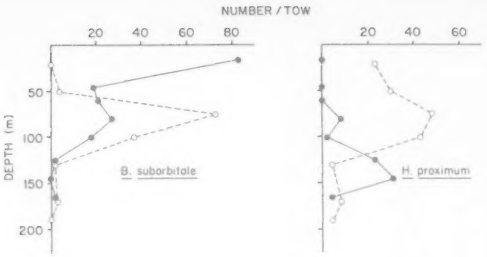

FIGURE 2.—Number of individuals of *Benthosema suborbitale* (left) and *Hygophum proximum* (right) caught per tow at several depths in the upper layers at night during new moon (solid circles and lines) and full moon (open circles, dashed lines) during September 1971.

Size composition and abundance showed a definite seasonal pattern. In June 1971, about 70% were 10-15 mm; there were a few adults and practically no intermediate sizes. The calculated size-frequency curves (Figure 3) shifted to the right from June to March indicating changes in size-composition due to growth. Though calculated day totals were higher than night totals for all but the June 1971 series, the rank order was the same for both, abundances being highest in December, lowest in June, and intermediate and nearly equal in September and March.

It appears that *B. suborbitale* spawns principally in the spring and summer. A few young (10-15 mm) are present by March and many by June. A substantial portion are 20-25 mm long

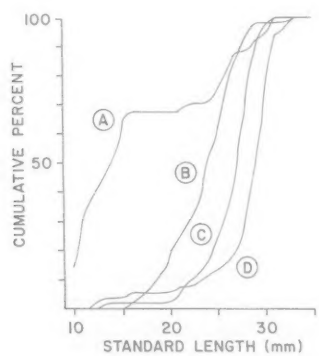

FIGURE 3.—Cumulative size-frequency curves for *Benthosema suborbitale* at four seasons. Size composition was calculated (see text) from samples taken throughout the water column in June 1971 (A), September 1970 (B), December 1970 (C), and March 1971 (D).

by September, but apparently not all have reached the minimum size caught by the trawl until later. Most fish are mature by December when maximum abundance occurs. There is apparently little growth in size between December and March and a decrease in total numbers. By June, most of the adults are gone and the next generation has begun to reach trawlable size. The percentages of mature females with ripe ova (Table 2) correlate with these trends; they were significantly higher in December and March, before the periods when juveniles appeared.

Benthosema fibulatum

B. fibulatum is apparently epibenthic or restricted to nearshore areas. In Hawaii, large individuals (45-95 mm) are regularly taken in bottom trawls at depths of 100-190 m at night (P. J. Struhsaker, pers. comm.), and large catches have been made by NMFS in CT tows at 25-100 m over areas where the bottom depth is about 600 m. Only eight of the individuals taken during this study were of the size taken by inshore trawls, 40-72 mm. The rest were 15-27 mm and mostly taken in the upper 100 m at night.

Diogenichthys atlanticus

D. atlanticus, although quite abundant in the Equatorial Pacific (Hartmann, 1971), was captured rarely in Hawaiian waters. About 80% of the individuals collected were adults, but the presence of 11- to 15-mm fish several times of the year suggests some spawning may occur in this area.

Hygophum proximum

In June 1971, nine small *H. proximum* (12-14 mm) were caught at about 650 m at night. As low as this catch was, it was higher than any shallow night catch and unlikely due to contamination. Similar numbers of this size were caught near this depth during the day and none in the shallow night tows, suggesting that the smallest *H. proximum* caught by the trawl do not regularly migrate. Individuals of this

size were, however, taken in shallow night tows during July 1970 and March 1971.

H. proximum appeared to avoid the IK at night more during new moon (see below) and was sampled best by the CT and by the full moon IK series. Both of these series indicated similar depth distribution but different trends in size composition with depth (Figure 4). In the CT series the curves for 75, 100, and 125 m were all similar and differed significantly from those at 25 and 50 m. Over 50% of the deeper catches were less than 30 mm, most about 20 mm. In the 25- and 50-m catches, which also differed significantly from each other, only 30% and 10% individuals were under 30 mm. Comparison of curves from IK catches at new moon during December and March 1971 also showed significant differences, with only the larger fish occurring above 50-60 m and smaller ones predominating deeper.

In the September 1971 series, the size-frequency curves for full moon tows at 25 and 50 m differed significantly from each other and

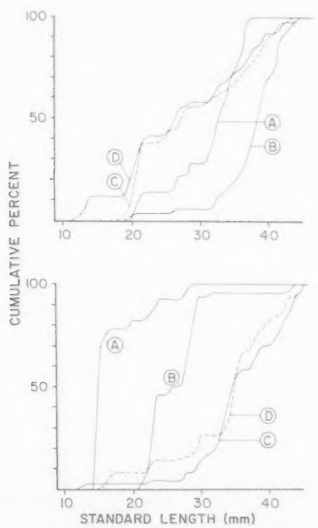

FIGURE 4.—Cumulative size-frequency curves for *Hygophum proximum* collected at different depths in the upper layers at night. Top: Cobb trawl samples taken at new moon during March 1971; depths of tows and number of individuals were: 25 m, 14 (A); 50 m, 150 (B); 75 m, 276 (C); and 100 m, 83 (D). Bottom: Isaacs-Kidd samples taken at full moon in September 1971 at 20 m, 23 (A); 50 m, 30 (B); 75 m, 48 (C); and 100 m, 43 (D).

from the curves at 75 and 100 m. The catch was almost all <15 mm at 25 m, 20-30 mm at 50 m, and over 30 mm for the deeper tows. In full moon tows during September 1970 at 80 and 100 m, the size-frequency curves differed significantly and indicated that most fish at 80 m were <30 mm and most at 100 m were >30 mm.

In the daytime during September 1970, size-frequency curves for *H. proximum* differed significantly, with a greater proportion of juveniles in shallower water. In March 1971 and June 1971, similar nonsignificant trends were present. All data indicated that individuals over 40 mm rarely occurred above 600 m.

At new moon during September 1971, high catches were made at 125 and 150 m with a few at 80 m (Figure 2). At full moon, catches were high between 20 and 100 m with practically none deeper. The calculated total for full moon was 3× that for new moon, and the calculated size-frequency curves indicated that new moon tows had missed most of the larger fish. These data, combined with the changes in size composition with depth, indicate that the smaller fish occur about 75-100 m deeper at new moon and the adults about 25-50 m shallower at new moon. The latter, however, appear to avoid the IK much more at new moon. Consequently, *H. proximum* was not sampled well by most IK night series.

The CT data also indicate that avoidance of the IK by larger fish was substantial. The calculated total for the CT series was 14.5× that for the March 1971 IK night series, and calculated size-frequency curves indicated much lower proportions of larger fish in the IK catches. The greatest difference was at 75 m where the IK caught only 5 as opposed to the CT's 276. Comparison of individual size-frequency curves indicated that some fish under 20 mm probably passed through the CT's meshes. Thus avoidance of the IK by larger fish is even greater than indicated by comparison of the calculated totals.

The calculated totals were much larger for the day series in March 1971 and June 1971, but day and night totals were close for September 1970 when the night tows in *H. proximum*'s depth range were taken during full moon. (Few were caught in December 1970 during day or

night.) Both of the September 1970 estimates were close to that for full moon in September 1971. Thus there appears to be less avoidance of the IK during the day than at night during new moon.

For March 1971, the calculated total from the CT series was only about 3.7× that of the day IK series, and the calculated size-frequency curves for the two series agreed closely. Thus the IK appears to sample *H. proximum* by day better than the CT at night. Since day tows and full moon night tows with the IK appear to sample this species about equally well, the IK may give better estimates of abundance and size composition than the CT at full moon. Kuba (1970) found that the IK sampled *H. proximum* better than the CT in night tows in equatorial waters. Most of his tows where this species was caught were taken near full moon.

The calculated day totals indicated that *H. proximum* was distinctly more abundant in September and March than in December or June. The calculated size-frequency curves for March 1971 and September of both years were similar and indicated that most fish were mature or nearly so. None less than 15 mm were caught in September or December, but a few 10-15 mm were caught in March 1971. Fish 12-14 mm long were present in fair numbers during the June 1971 series and abundant in July 1970. This suggests that *H. proximum* spawns principally in spring or early summer. The percentages of mature females with developed ova were highest in March and June but did not differ significantly from the other values.

Hygophum reinhardti

H. reinhardti was less abundant and occurred slightly deeper than its congener, *H. proximum*, but the data indicated that similar sampling problems existed. So few *H. reinhardti* were caught in the March 1971 IK series that it was impossible to make quantitative comparisons with the CT data, but it appeared the IK missed substantial numbers at 75-100 m and sampled about as well as the CT in deeper water. Though catches were low during both September 1971 series, the full moon series caught overall higher numbers and indicated a shallower night depth than the new moon series. In all four regular series, catches of day tows were generally higher than those of night tows.

Size-frequency curves from the CT series indicated no trends in size composition with depth. The curves for IK tows in September 1970 at 150 and 195 m differed significantly with few fish >20 mm at 195 m and few <20 mm at 150 m. Three-day tows in September 1970 showed no individuals over 20 mm at 520 m and most over 20 mm at 775 and 900 m. There were no obvious seasonal changes in abundance. Juveniles (<15 mm) and females with developed ova were present at all seasons.

Myctophum spp.

Three species of *Myctophum*—*M. nitidulum*, *M. obtusirostrum*,[5] and *M. spinosum*—apparently occur at or near the surface at night. They were regularly dipnetted at the surface at night, but few were caught in the trawls, even in preliminary tows at 10-m depth. Individuals considerably larger than the trawl-caught specimens were frequently taken by dip net. These species are relatively solid-bodied and are probably strong swimmers. They probably avoid the trawl easily in the process of avoiding the ship itself.

The few day catches of these species were mostly from 500 to 800 m but may well have been due to contamination. These species are distinctly countershaded, and in life the upper color is quite blue, suggesting that they occur at shallow, well-lighted depths during the day where they can avoid the trawl. Nevertheless, the rarity of even small individuals in the trawl catches indicates that none of the three were abundant.

Myctophum selenoides

At night, small (<30 mm) *M. selenoides* were taken mostly between 50 and 100 m. The larger fish were below 100 m and mostly around 150 m. Only three were taken during the day, one by

[5] *Myctophum obtusirostrum* is the correct name for the species called *M. branchygnathum* by Nafpaktitis and Nafpaktitis (1969) and others (B. G. Nafpaktitis, pers. comm.).

CT at 300 m and two by IK at 500 m. The low numbers of juveniles as well as adults in the trawl catches suggest that rarity of *M. selenoides* was not due to avoidance. Small fish (8-13 mm) were caught only in March and June 1971, indicating that this species spawns locally—probably in the spring.

Symbolophorus evermanni

The larger individuals of *S. evermanni* are undersampled by the IK. Kuba (1970) showed this in Equatorial Pacific waters. During March 1971 CT catches were 28-35/tow as compared with 1-2/tow for the IK at similar depths. The CT tows indicated that *S. evermanni* was most abundant at 50-100 m at night and showed no differences in size frequency with depth. On one occasion, November 1969, several large individuals were dipnetted at the surface.

Day tows with the IK caught no individuals above 500 m and most between 600 and 800 m. A few substantial catches, 6-8/tow, came from 800 to 900 m. There was some indication that fish <20 mm do not regularly migrate; particularly in September 1970, most of the shallow catches were larger fish, and most small individuals were taken in night tows around 800 m.

Centrobranchus choerocephalus

Most catches of *C. choerocephalus* were at 550-650 m during the day. The night depth appeared to be between 100 and 200 m for both IK and CT samples, but on one occasion, September 1969, seven individuals were dipnetted at the surface.

Lobianchia gemellari

L. gemellari was never taken in large numbers. At night, all individuals caught above 100 m were <25 mm, and those over 40 mm were caught only below 150 m. The CT series, which caught fair numbers, also showed this trend with significant differences in size-frequency curves. Substantial catches of larger fish were made as deep as 300 m at night, but there were no differences in sex ratio or percentage of ripe females between deep and shallow catches of adults.

There was no evidence that this species avoided the IK better than the CT nor that there was a day and night difference in avoidance of the IK. Also the depth distributions and abundances in full and new moon were not grossly different.

The pooled IK data indicated that juveniles, <25 mm, were most abundant in the summer (July 1970, June 1971) and least so in December 1970. Curiously, there were few juveniles present in September 1970 but many in September 1971. Adults were most abundant in March 1971 when few juveniles were present.

Lobianchia urolampa

Only two juvenile *L. urolampa* were taken in this study. This species is apparently nearshore or epibenthic. Adults (48-99 mm) have been taken in bottom trawls at depths between 124 and 190 m at night (P. J. Struhsaker, pers. comm.).

Diaphus bertelseni

The identity of this form with the Atlantic *D. bertelseni* is not certain since only one large individual was taken. The species was caught on only two occasions. Many were taken in the March 1971 series including 70 in one CT tow at 125 m at night. One each was taken at 300 and 400 m with the CT during the day suggesting that this species has a shallow day depth. All March 1971 specimens were between 17 and 31 mm—most between 17 and 25 mm. The only other individual taken was a 38-mm specimen from 100 m at night during the July 1970 series.

Diaphus "glandulifer"

The form designated here as *D.* "glandulifer" appears to be an undescribed species (R. L. Wisner, pers. comm.). Gill raker counts were mostly 8+1+15−16, lower than those for *D. glandulifer* from the Western Pacific (Wisner, see footnote 3). Accessory luminescent tissue occurred regularly in specimens over 30 mm

at POL, VLO, SAO-3, Pol, and Prc-4. In 8 out of 20 specimens over 50 mm, there was accessory tissue at PO-4, VO3, or both.

Only small (<20 mm) *D.* "glandulifer" were caught above 150 m, the larger individuals being around 200 m and deeper at night. This species was rare at all seasons, and most specimens were either in a 27-39 mm group or over 45 mm. Catches of a few less than 20 mm suggest that this species may occasionally spawn in the area.

Diaphus schmidti

There was no indication that any sizes of *D. schmidti* sampled by the trawl did not regularly migrate to the upper layers at night. There were significant differences in size-frequency curves from different depths at night. The number and percentage of juveniles (<25 mm) were greatest around 25 m. The number of larger fish was greatest at 50 m, but the percentages of small and large fish were roughly equal. At 75-80 m most or all the individuals were larger. Only the day samples from March 1971 were spaced closely enough to suggest that there were similar size-frequency changes within the day depth range.

Because *D. schmidti* occurred over a relatively narrow depth range during the day and was frequently caught in only one tow per series, it was impossible for some series to assign realistic weighting factors for calculation of total numbers. However, the calculated night size-frequency curves agreed closely with those of the day samples.

The calculated size-frequency curves for CT and IK in March 1971 agreed quite closely, but the calculated total for the CT was 15× that of the IK. The difference in totals was due to relatively much greater catches by the CT at 75 and 100 m. The CT caught only 1.7 and 6.3× the IK at 25 and 50 m, but caught 65 and 45× more at 75 and 100 m, respectively. The pairs of individual size-frequency curves at 25 and 50 m differed significantly and indicated that the IK caught more larger fish, while the curves at 75 and 100 m from the CT did not differ from those of the IK at 80 m. Since both large fish and juveniles occurred shallower and only large fish deeper, it appears that the CT undersampled larger fish in shallow zones and the IK undersampled them in deeper zones.

The full moon samples indicated that peak depth was around 75 m and caught none at 20-50 m where new moon tows indicated maximum abundance. The calculated total for full moon was about three-fourths that of new moon, and the calculated size-frequency curves indicated a somewhat larger proportion of juveniles during full moon. Thus *D. schmidti* occurs deeper at full moon, and larger individuals may avoid the net more frequently.

D. schmidti apparently spawns in late spring and summer and matures in about 1 year. In June 1971, the population consisted mostly of either juveniles or adults with few individuals between 20 and 30 mm. Both juveniles and 20- to 30-mm individuals were present in September 1970 and 1971. In December 1970, almost all were 20-30 mm, and in March 1971, almost all were over 30 mm. Percentages of ripe females were significantly higher in the March and June 1971 series than in the September 1971 series. Practically none were mature in December 1970.

Diaphus fragilis

D. fragilis was caught most frequently at night at 25-50 m (new moon) and 100-125 m (full moon). The CT catches were low and did not indicate that this species was avoiding the IK in appreciable numbers. *D. fragilis* was distinctly more abundant in September 1970 and 1971 and least so in December 1970 and March 1971. It is one of the dominant species of myctophids in Pacific equatorial waters (Hartmann, 1971) but its presence in low numbers near Hawaii cannot be ascribed entirely to immigration. Fair numbers of small (<20 mm) individuals were caught in September, suggesting that some spawning occurs in the summer.

Diaphus rolfbolini

Pooled size-depth data indicated that *D. rolfbolini* <20 mm occurred principally above 100 m, those 20-45 mm around 100 m, and

those over 45 mm below 12[7] m. *D. rolfbolini* was caught in roughly similar numbers at all seasons; however, trends in size composition were evident from the pooled data. In July 1970, September 1970 and 1971, and June 1971, 50% or more of the catches were <20 mm. In December 1970, almost all were between 20 and 40 mm, and in March 1971, both CT and IK catches were mostly between 45 and 55 mm. Individuals over 55 mm were present in low but consistent numbers all year round and may be more than 1 year old.

Diaphus elucens

D. elucens showed definite changes in size composition with depth at night. Size-frequency curves from the CT series in March 1971 differed significantly. There were two size groups present at that time, 32-47 mm and 49-63 mm. The smaller size group made up 80%, 73%, and 20% of the catches in tows at 50, 75, and 100 m, respectively. The number of smaller fish was roughly equal in the two shallower tows and those of larger fish comparable in the two deeper ones. In September 1971, full moon, 98 individuals 7-11 mm long were caught at 20 m, and 12 of 13-17 mm at 50 m. Few of these sizes were taken in deeper water where some larger individuals were caught. No trends could be recognized in the daytime samples.

The pooled IK data indicated that *D. elucens* spawns in late summer and reaches maturity in about 1 year. In June 1971 and July 1970, most individuals were over 40 mm. In September 1970 there were two distinct size classes, 10-13 mm and over 46 mm with practically none in between. In September 1971, new moon, there was a broad group 10-29 mm and a few over 50 mm. In the full moon series, there was a distinct group at 7-11 mm, a smaller group at 12-18 mm, and practically none larger. In December 1970, 70% were 23-41 mm, and in March 1971, the two size groups mentioned above were present in both IK and CT data.

Diaphus sp. A and B

D. sp. A and B are superficially similar to each other and resemble most closely *D. mollis* from the Atlantic, but both appear to be distinct species. All but the smallest specimens can be readily distinguished. Species A has a rounded opercular margin, and the eyes of Formalin-preserved specimens are distinctly green. In species B, the upper opercular margin is distinctly angular or hooked, and the eyes are yellow-white. The counts for fully developed gill rakers were usually 4+1+10 for species A and 5+1+10−12 for species B. Species B matures at and reaches a much larger size than species A.

Species A was taken in abundance (>10/tow) only 13 times, and size-frequency curves could be compared only for samples from the July 1970 and March 1971 CT series. These both indicated significant differences with the smaller fish occurring in shallower water. The one daytime comparison possible, in September 1970, showed no difference between tows at 500 and 575 m. There was no evidence that any sizes did not migrate regularly.

There were no obvious differences in abundance and size frequency between day and night tows. Two CT tows in March 1971 caught species A similar in size composition to the two positive IK tows, but the CT catches were highest at 50 m and substantial at 75 m whereas the IK indicated a peak at 25 m and only a few at 50 m. At new moon, the depth of highest catch was at 45 m and at full moon was at 75 m. The catch at new moon was about 5× that at full moon, indicating greater avoidance as well as depression during full moon.

Abundance was distinctly higher during July 1970 and September 1970 and 1971 with the largest proportion of small fish at these times. Abundance was distinctly lowest in June 1971 and almost all were adults. These data suggest that species A spawns in the summer and reaches maturity in about 1 year. However, the condition of the ovaries did not indicate a restricted spawning season; 89-100% of the mature females were ripe at all seasons (Table 2).

Only the juveniles (<15 mm) of species B occurred above 100 m. Abundance was highest in June 1971 and most of the catch was juveniles

at that time. Juveniles were also present in July 1970 and September 1971.

Diaphus anderseni

At night, adults of *D. anderseni* occurred mostly around 200 m whereas the juveniles (<13 mm) were found only around 100 m. *D. anderseni* had one of the shallowest day depths (Table 1) and most limited migrations of all the species considered, the adults covering only about 100-200 m each night. In all series but March 1971, catches were mostly small juveniles and adults, but in March 1971 both CT and IK tows indicated the population was composed entirely of intermediate-sized fish. Apparently this species spawns over the greater part of the year.

Diaphus brachycephalus

Numbers of *D. brachycephalus* were quite low except in September 1970 when large numbers of juveniles (<20 mm and most <15 mm) were collected around 50 m at night. The larger individuals caught at 150-200 m were mostly females. Five of the 10 larger males (over 40 mm) taken at night were caught below 300 m, suggesting that the larger males migrate little or not at all. Presence of 9- to 12-mm fish in June, July, and September and their absence in December and March indicated that *D. brachycephalus* spawns in the summer. The June and September samples included both very small and adult fish; the March samples were mostly intermediate sizes (15-30 mm) suggesting that this species reaches adult size within 1 year.

Diaphus adenomus and *D. chrysorhynchus*

D. adenomus and *D. chrysorhynchus* are both apparently epibenthic and associated with shallow water. *D. chrysorhynchus* (54-98 mm) is frequently taken in bottom trawls at 75-190 m at night and *D. adenomus* (41-153 mm) at 180-185 m at night. Both are taken down to 500-600 m during the day (P. J. Struhsaker, pers. comm.). Individuals of the sizes taken near the bottom were rarely caught in midwater. The *D. adenomus* were all taken during the day by IK. Thirteen of the *D. chrysorhynchus* collected were larger fish (56-84 mm). These were taken sporadically at all seasons, eight of them in the upper layers at night. The remaining 21 specimens were all 11-17 mm and all taken in the upper layers at night during the September 1971 series, 11 of them in one tow at 80 m. This suggests that this species spawns in late summer and that the young are pelagic. Unless substantial numbers of adults of these species are able to avoid both CT and IK, it appears that the larger fish caught pelagically were wanderers.

Notolychnus valdiviae

Significant differences in size-frequency curves from several series indicated that smaller *N. valdiviae* occurred higher in the water column. In both September 1970 and 1971 series, the catch at night at 80-100 m was almost totally <15 mm and at 115-145 m mostly over 20 mm. In other series, single pairs differed significantly, but trends were not as obvious because most of the fish were of one size class. Two day tows in September 1970 at 525 and 725 m also differed significantly with 60% of the fish <20 mm in the shallow tow and over 90% >20 mm in the deep tow.

In September and December 1970, night catches of *N. valdiviae* near the day depth were larger than that expected from contamination. Substantial catches were also made in the upper layers during these series. In September 1970, roughly 70% of the population remained at depth. There were relatively more larger fish in the nonmigrating fraction (Figure 5). In December 1970, roughly 50% did not migrate, but there was little difference in size composition between shallow and deep catches. There were no significant differences in either sex ratio of mature fish or ripeness of mature females between the shallow and deep night catches. There was no indication that any sizeable fraction of the population did not migrate in either March or June 1971.

The calculated totals for day and night agreed fairly closely and indicated no differential avoidance. Likewise, the calculated size-

frequency curves were quite similar. The agreement of numbers and curves was closest for June 1971. This indicates that since the night data were all from shallow tows, most, if not all, of the population migrated at that time. There was little point in comparing CT-1K data since most fish were apparently small enough to pass through the coarser CT meshes.

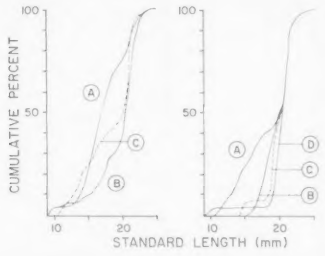

FIGURE 5.—Cumulative size-frequency curves calculated for *Notolychnus valdiviae* (left) from samples taken during September 1970 in the upper layers at night (A), near the day depth at night (B), and during the day (C); and (right) from samples taken throughout the water column in September 1970 (A), December 1970 (B), March 1971 (C), and June 1971 (D).

The new moon series in September 1971 indicated the population was mostly between 75 and 145 m while at full moon it was between 130 and 190 m. The calculated size-frequency curves agreed closely, but the new moon series calculated total was about 3× that of full moon. This suggests that *N. valdiviae* occurs about 50 m deeper and avoids the net better during full moon. The latter seems questionable since even adults are quite small and unlikely to avoid the trawl. Although full moon tows below 200 m in other series made no substantial catches, it is possible that some of the population was below the deepest depth sampled during the September 1971 full moon series.

Both day and night calculated totals indicated that *N. valdiviae* was distinctly most abundant in September and least so in March; the values for December were slightly higher than those for June. Both September series indicated large proportions and numbers of smaller (<15 mm) fish. A few small fish were present in March and June, but in December none were <17 mm (Figure 5). The percentages of mature females with developed ova for March and June were significantly higher than those for September and December.

Lampadena luminosa

No individuals of *L. luminosa* over 32 mm were caught above 100 m at night, but a few, 16-24 mm, were taken shallower. The rest of the catches, of both large and small fish, were mostly between 150 and 250 m. Five fish, 16-18 mm, were taken during the day at 525-550 m, but most day catches of all sizes were between 650 and 750 m. In June 1971 and July 1970, the catch was almost exclusively <25 mm fish; in September these small fish still predominated but there were also several 25- to 40-mm individuals caught. Only one specimen was caught in December 1970, and in March 1971, 80% of the catch was over 35 mm. None of the individuals captured were mature, suggesting that the adults are larger than the maximum size collected and likely take more than 1 year to mature.

Lampadena urophaos

L. urophaos was caught rather sporadically; only one each was caught at night in September and December 1970, and none during the day in December 1970 or June 1971. All sizes appeared to be present throughout the ranges given. One fish 18 mm long was caught in December and several <30 mm were taken in March, June, and July. Otherwise, most of the fish were 35-65 mm with a few individuals over 90 mm. One ripe female, 98 mm, was collected in March.

Taaningichthys bathyphilus

T. bathyphilus was taken regularly between 600 and 1,000 m and occasionally deeper both day and night. Highest catches were between 700 and 800 m. It was the only myctophid which definitely did not migrate. Size composition of the catches was roughly similar at all seasons with most individuals 30-60 mm long.

Taaningichthys minimus

Other reports, e.g., Davy (1972), have stated that *T. minimus* does not migrate, but all night catches in this study were well above the day depth range. Individuals 20-30 mm long were caught between 150 and 250 m at night and larger fish between 200 and 400 m. None were taken in night tows below 475 m. Of 32 fish caught in March 1971, 27 were 20-24 mm and only 1 was over 50 mm. In other seasons, all were over 30 mm, and most over 50 mm, suggesting that *T. minimus* spawns principally in late winter or early spring. Too few mature females were taken to correlate gonad ripeness with the changes in size composition.

Lampanyctus niger

Most *L. niger* less than 25 mm long were taken at depth both day and night, indicating that the majority of the smaller fish do not regularly migrate. In December 1970, no individuals under 50 mm were caught in the upper layers, and large catches with about 50% larger than 50 mm were taken near the day depth at night (Figures 6 and 7). The mature individuals taken in deep night samples did not differ from those of shallower samples in sex ratio or percentage of ripe females. Smaller peaks at depth during the night were present during other series, but catches of fish over 25 mm could not be discriminated from contamination.

In the upper layers at night, the size-frequency curves from catches above 150-165 m were usually significantly different from those in deeper tows (Figure 7). Few individuals over 50 mm were caught above 165 m, and below 200 m, 50-100% of the catches were over 50 mm. Similar stratification by size was evident in some day series and suggested, nonsignificantly, that individuals less than 50 mm rarely occurred deeper than 750 m.

The calculated totals for day and night agreed well for all but the June 1971 series (day was 1.6× night). The calculated size-frequency curves differed greatly for the September 1970 and June 1971 series. The difference for September 1970 may well have been due to missing

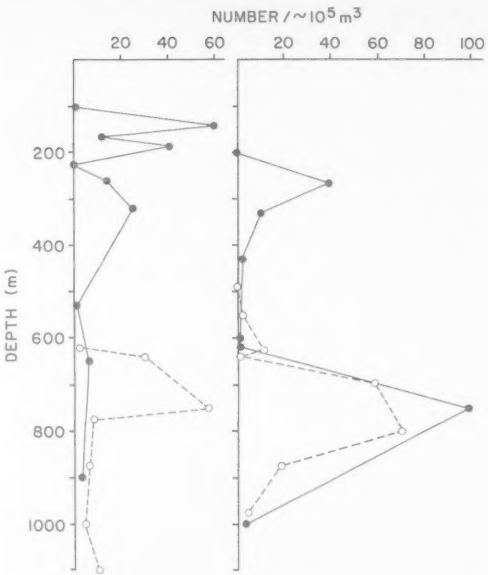

FIGURE 6.—Depth-abundance profiles for *Lampanyctus niger* from samples taken by Isaacs-Kidd trawl during June 1971 (left) and December 1970 (right). Night samples are designated by solid circles connected by solid lines; day samples by open circles and dashed lines. Numbers collected were adjusted to a 2-hr towing time with volume filtered of ca. 10^5 m^3.

juveniles at depth at night. The discrepancies for June 1971 were principally due to an exceptionally large catch of 30- to 36-mm fish at 140 m at night.

L. niger, especially the larger individuals, apparently avoided the CT more than the IK. The ratio of CT to IK catches was low (1.2-5.8) for all depth pairs except at 100 m where the CT caught 18 to only 1 in the IK. The calculated total for the CT was only 2.3× that for the IK tows above 200 m. The individual size-frequency curves were significantly different in three of four pairs but not consistent in direction. The calculated size-frequency curves indicated that the CT caught lower percentages of 50- to 70-mm individuals.

During the new moon series, *L. niger* was caught at 145 and 165 m—the deepest samples, but at full moon none were caught. It is not known whether all of the population occurred below 190 m, the deepest depth sampled at full moon, or whether there was increased avoidance.

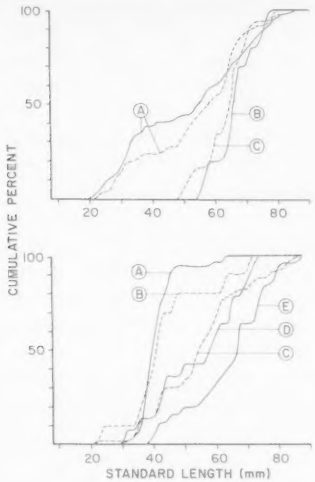

FIGURE 7.—Cumulative size-frequency curves for samples of *Lampanyctus niger* collected at different depths at night. Top: December 1970—two samples from 750 m of 119 and 174 individuals (A); 320 m, 10 (B); and 250 m, 39 (C). Bottom: June 1971—140 m, 60 individuals (A); 165 m, 12 (B); 185 m, 41 (C); 260 m, 14 (D); and 300 m, 25 (E).

The calculated totals indicated for both day and night series that *L. niger* was most abundant during December 1970; the figures for other series were all similar and about one-half of those from December 1970. Except for slightly higher percentages of smaller (<40 mm) fish in December and September 1970, there were no distinct differences in the calculated size frequencies. The percentages of mature females with developed ova for both December 1970 and March 1971 were significantly higher than those for June 1971 and September 1970. Together these data indicate that *L. niger* spawns principally in the early part of the year and that most of the juveniles are recruited to the trawlable population by December.

NOTE (Added in press)

The name *Lampanyctus niger*, used above, included both individuals with weakly developed pectoral fins and those without pectoral fins. Recently, M. A. Barnett informed me that, in specimens collected north of Hawaii, there are differences in other features which correlate with the presence or absence of pectoral fins. All of our specimens have been reexamined and, regrettably, there appear to be at least two forms present. The taxonomic status of these forms cannot be evaluated. A world-wide revision of species of the *Lampanyctus niger-ater-achirus* complex will be necessary to fully elucidate the problem (cf. Nafpaktitis and Nafpaktitis, 1969). Consequently, the text above was left unaltered, and the following supplementary data is offered here. The latter must be regarded as tentative since it was impossible to identify all specimens with certainty due to damage during collection.

Roughly one-half the specimens have no pectorals. These, designated as Form A, also differ from the others in that the PVO_2 photophore is well separated from PVO_1 and above the level of PO_4. The SAO_3 is usually posterior to AOa_1, and AOa + AOp is 5-6 (rarely 4) + 6-7 (rarely 8) = 12-13 (rarely 11). Form A appears to reach maturity at about 57-58 mm and reaches a maximum size of 74 mm.

In the remaining specimens, the pectoral fin was variously developed but always present. The PVO_2 was closer to PVO_1 and at or below the level of PO_4. SAO_3 was usually anterior to or above AOa_1. The majority of these had AO counts of 5(4) + 6(7) = 11. These, Form B, reached maturity at about 70 mm, and the maximum size was 84 mm. Among the specimens with pectorals, the eleven largest individuals (85-125 mm) and about two percent of the smaller ones had higher AO counts—5-6 + 6-7 (rarely 8) = 12-13 (14). None of these larger fish were mature, suggesting the presence of a third form, Form C.

Thus there appear to be two very similar forms that were common and roughly equal in abundance and a larger, much rarer form. The depth distributions, migrations, size-depth patterns, and seasonal changes of Forms A and B are quite similar and essentially as described above under *Lampanyctus niger*. The co-occurrence in abundance of two such similar forms contrasts with the patterns of most other closely related species. Further investigation of not only the taxonomic status, but also the geographic distribution of these forms will be necessary to determine if, as with the *Hygophum*

spp., Hawaii is near the edge of their ranges. Little can be said about Form C; it appears to have a depth distribution and migration pattern similar to those of the other two.

Lampanyctus nobilis

L. nobilis apparently does not begin migrating until about 25-30 mm long. A few small fish were taken in shallow tows at night, but most were taken at 625 and 750 m at night during September and December 1970. The absence of small individuals in deep night tows during March and June 1971 was probably due to widely spaced sampling since substantial numbers of small ones were caught in day tows then. There was no evidence that other sizes did not migrate regularly.

There were few instances where enough *L. nobilis* were taken to make comparisons of size composition and depth, but several pairs of size-frequency curves showed significant differences. Individuals <30 mm were mostly above 75-80 m at night, and most fish below 100 m were >40 mm. All night catches of exceptionally large individuals (16 of >95 mm) were below 100 m. During the day, catches above 750-800 m were almost all <25-30 mm, and the only substantial catches of fish >40 mm were at 1,150 and 1,200 m in September 1970. The only mature individual caught during the day, 100 mm long, came from a tow at 1,250 m. It is possible that the lower end of the day depth range was not adequately sampled.

L. nobilis avoids the IK in substantial numbers. In March 1971, the CT tows indicated a depth range similar to that of the IK series (Figure 8), except that a large catch was made at 175 m, below a catch of almost none at 150 m. The size-frequency curve from the 175 m CT tow looked like a composite of the shallower tows. This catch was likely due to excessive contamination and was disregarded. The calculated total for CT was 18× that for the IK principally due to catches at 100 and 125 m which were 21.4× and 24.8× the IK catches at these depths. The size-frequency curves for individual pairs differed significantly and like the calculated total curve indicated that the IK missed individuals over 40-45 mm. Thus

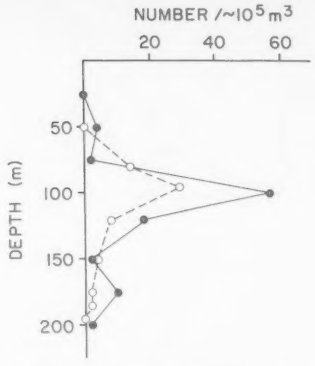

FIGURE 8.—Estimates of abundance of *Lampanyctus nobilis* at different depths at night during March 1971 from samples with the Cobb trawl (CT) (solid circles and lines) and Isaacs-Kidd trawl (IK) (open circles, dashed lines). CT catches were adjusted to the same volume filtered by 2-hr tows with the IK, ca. 10^5 m^3.

L. nobilis was probably about twice as abundant as the IK tows indicated.

At new moon in September 1971, *L. nobilis* occurred between 60 and 125 m with peak abundances at 75 and 100 m. At full moon, the only individual caught was from 190 m. Tows below 200 m taken during full moon in other series made no substantial catches. Thus the difference between the new and full moon series was probably due to greatly increased avoidance at full moon.

There were no gross seasonal differences in abundance or size composition apparent from the IK data except that *L. nobilis* may have been slightly less abundant in June 1971. Small (<25 mm) fish were present in comparable numbers in September 1970, December 1970, and June 1971 (the proper depth zone was not adequately sampled in March 1971 day or night).

With the exception of a 78-mm individual, all ripe females were over 97 mm and were rarely caught—once in September, once in March, and twice in June. The presence of juveniles indicated that spawning regularly occurs in the area, and the presence of immature sizes in fair abundance suggests that adults should be more abundant than catches of either IK or CT indicated. It seems likely that these larger fish avoided both trawls in substantial numbers.

Lampanyctus steinbecki

All postlarval *L. steinbecki* appeared to migrate regularly. Within the night and day depth ranges, the size-frequency curves were usually displaced to the right with increasing depth (Figure 9). The differences were significant only in September and December when several size classes were present in abundance. In these cases the differences were due to changes in absolute numbers of both small and large individuals, the shallower samples being composed almost entirely of juveniles and the deeper ones of adults only. Consistent, significant differences in size-frequency curves of day samples indicated that adults (>40 mm) occurred mostly below 850-900 m and few smaller fishes occurred at these depths.

The percentages of females among mature fish tended to decrease with depth in the March 1971 night samples. The values for samples from 95, 120, 135, 175, and 265 m were 82, 63, 64, 55, and 44%, respectively. The only significant differences were between the highest value and the two lowest ones. There were some significant differences among the June 1971 night samples, but no trend with depth was evident.

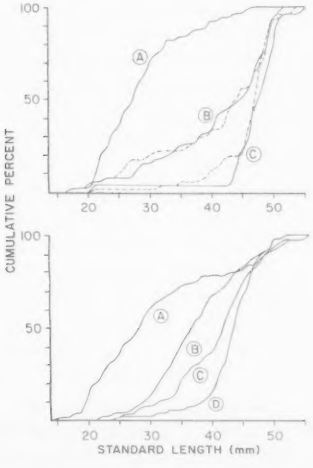

FIGURE 9.—Top: Cumulative size-frequency curves for samples of *Lampanyctus steinbecki* collected at night during new moon, September 1971, at depths of 80 m, 58 individuals (A); 100 m, 59 (B, solid line); 125 m, 46 (B, dashed line); 145 m, 49 (C, dashed line); and 165 m, 28 (C, solid line). Bottom: Cumulative size-frequency curves for *L. steinbecki* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

The calculated totals were higher for the day series in all cases. The day totals were relatively highest for the September and December 1970 series (2× and 1.6× night totals, respectively) and were probably in part a result of poor timing of the night samples with respect to moon phase. For March and June 1971 the day totals were about 1.5× higher than night. Except for December 1970 the calculated size-frequency curves for day and night series were quite similar. Thus all sizes appear to avoid the IK better at night.

The individual CT tows caught from 0.7 to 4.5× their paired IK tows, and there was no obvious trend in differences of the size-frequency curves. The calculated curve for the CT was displaced slightly to the right of both night and day IK curves for March 1971, but the calculated CT total was only 3.4× the night IK total. Apparently *L. steinbecki* avoids the CT more than the IK.

During new moon in September 1971 the peak depths were at 80 and 100 m, and at full moon none were caught above 120 m. The catches at 170 and 190 m at full moon both exceeded the peak catches at new moon. The water column totals were nearly equal, but the full moon calculated curve and the individual curves were displaced far to the left of new moon curves indicating substantially greater numbers of 20- to 40-mm individuals. The new moon tows seemed to miss substantial numbers of juveniles; and if large numbers of larger fish occur below 190 m at full moon (there was some evidence for this from full moon tows in other series), it is possible that full moon tows may also sample the larger fish better. The increase in night depth with full moon, about 100 m for the juveniles, was about twice that observed for other species.

Both day and night calculated totals indicated that *L. steinbecki* was least abundant in March 1971 and present in comparable numbers during the rest of the seasons. The calculated size-frequency curves (Figure 9) indicated that 80% of the individuals were immature in September

1970, with 50% under 30 mm. In December 1970, most fish were still immature, but the peak size group was 30-40 mm. In March and June 1971, about 65 and 90% of the fish, respectively, were mature. The percentages of ripe females among mature females were highest in March and June 1971 and were significantly lower than all others in December 1970. Thus *L. steinbecki* appears to spawn principally in the spring and summer and to reach trawlable size by September. Most fish appear to live about 1 year.

Lampanyctus tenuiformis

L. tenuiformis differs from *L. steinbecki* principally in size at maturity and relative positions of a few photophores. Counts of fin rays, etc., for the two species were either identical or overlapping. Individuals over about 40 mm could be distinguished by the relative development of the gonads, but it is possible that some smaller, damaged *L. tenuiformis* were erroneously identified as *L. steinbecki*. Owing to the former's rarity, as evidenced by the few larger individuals, any error is almost certainly negligible.

Only four *L. tenuiformis* were taken at night, and the larger two of these (120 and 138 mm) were taken in tows near the day depths. Thus the night depth range given in Table 2 is quite uncertain. *L. tenuiformis* appears to spawn near Hawaii; four females (123-138 mm) with ripened ova and two small juveniles (28 and 32 mm) were collected.

Triphoturus nigrescens

T. nigrescens <15 mm were caught only in a night tow at 650 m in June 1971, suggesting that small juveniles do not migrate. In December 1970, high catches of larger fish were made during the night both in the upper layers and at the day depths. Calculated totals indicated roughly 60% of the population did not migrate. Calculated size-frequency curves for shallow night, deep night, and day samples all were quite similar and also agreed closely with the curve from fish taken in three short night oblique tows from 0 to 300 m. Differences in sex ratio and percentage of mature females with developed ova between the deep and shallow samples were small and nonsignificant.

Large numbers of more than one size class were caught only in July and September 1970. There were significant differences between size-frequency curves indicating that fish <20 mm occurred mostly above 50 m at night and above 650 m during the day. Adults occurred mostly below 50 m at night and below 650-700 m during the day.

Owing to low numbers in June 1971 and poor timing of shallow night tows in September 1970, day and night comparisons could be made only for December 1970 and March 1971. The day calculated totals were larger in both series, 1.3× for December 1970 and 3.8× for March 1971. The larger discrepancy in March 1971 may have been due to missing nonmigrating fish at night. The calculated size-frequency curves for day and night agreed closely.

The CT tows in March 1971 caught only 2.5-4× the IK tows; the calculated total for the CT was 2.6× that for the IK night series. The calculated size-frequency curve for the CT was nearly identical to both the day and night IK curves, and most fish were over 30 mm. Apparently *T. nigrescens* is better able to avoid the CT, but it is possible that some fish of even the larger sizes could have escaped through the coarser CT meshes.

T. nigrescens appears to have a 1-year generation cycle with spawning principally in spring and summer. Abundance was distinctly highest in December and extremely low in June and September 1971 with substantial and roughly equal numbers present in September 1970 and March 1971. *T. nigrescens* was also abundant in July 1970 with most of the population either adults or <20 mm. In September 1970, 65% of the population was 20-28 mm with few adults, and in December, 85% were over 25 mm. In March 1971, 85% were over 30 mm and none <24 mm. In June 1971, the catches were made up almost entirely of adults or fish <15 mm. The conditions of the ovaries were correlated with the changes in size frequency. The percentages of mature females with developed ova (Table 2) were low

in September and December 1970 and were significantly higher in March and June 1971.

The decline in abundance observed for *T. nigrescens* in June and September 1971 was the most dramatic change observed among all the species during the study period. The difference between the series in July and September 1970 and those of June and September 1971 suggest that either spawning success or larval survival was markedly lower in 1971. The only obvious factor correlated with this change was a significant increase in the percentage of females among mature fish in June 1971. Whether there was a causal relationship between the two changes cannot be determined from the data.

Bolinichthys longipes

Apparently almost all *B. longipes* of the sizes sampled regularly migrate. The only indication of nonmigration was a catch of seven small (12-14 mm) individuals at 650 m during the night in June 1971; individuals of these sizes were caught frequently during the day tows but rarely at night in the upper layers suggesting that some small individuals do not migrate. Within each series there were relatively few significant differences between size-frequency curves of the separate tows. These indicated that the smaller fish tended to be found shallower at night. Differences between day tows clearly indicated (Figure 10) that few fish less than 20 mm occurred deeper than 625 m and few larger than 30 mm occurred above this depth.

In the March 1971 night samples, the percentages of females among mature fish decreased with depth. The values were 73% at 80 m, 59% at 95 m, 32% at 120 m, and 46% at 135 m. The first two values were significantly different from the latter two. Insufficient mature fish were caught to compare values at different depths in other series.

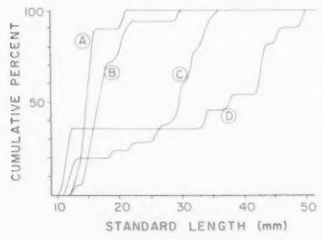

FIGURE 10.—Cumulative size-frequency curves for samples of *Bolinichthys longipes* collected during the day during June 1971 at depths of 560 m, 11 individuals (A); 600 m, 18 (B); 620 m, 21 (C); and 640 m, 11 (D).

The calculated totals agreed well for the day and night series, but calculated size-frequency curves differed for almost all pairs. Depth coverage was best for the March and June 1971 series, and the calculated curves were closest for the March 1971 series. The curves for the June 1971 series differed mostly because of a greater frequency and number of small individuals in the day. The numbers caught were quite low for all tows of this series, and inclusion of seven small individuals from a deep night tow (see above) in the calculations brought both the calculated totals and curves into very close agreement for the June 1971 series.

The CT tows indicated that peak depth was at 75-100 m and caught fair numbers of *B. longipes* at 25-50 m where the IK caught few or none. The IK peak depth was at 100 m and substantial numbers were caught at 125 and 135 m where CT catches were relatively low. The ratios of CT to IK numbers were 9.4 and 5.6 at 75 m and 100 m, respectively, but only 1.1 at 125 m. The calculated CT total was 5× that for the IK. The IK and CT size-frequency curves were similar at 75 m but differed significantly at 100 and 125 m due to larger percentages of fish over 35 mm in the CT catches. The calculated CT curve was displaced to the right also due to higher percentages of fish over 35 mm. Thus it appears that the CT sampled *B. longipes* as well or better than the IK above 100 m, but in the deeper zones the IK gave higher estimates of abundance in spite of missing some larger fish.

At new moon, *B. longipes* was abundant between 60 and 125 m and peaked at 80-100 m. At full moon, practically none were caught above 130 m and the peak was at 170-190 m. Full moon tows in other series indicated that few occurred deeper. The new moon catch at 60 m and the full moon catches at 130 and 170 m were similar in size composition; almost all fish were <20 mm. The 190-m curve at full

moon resembled those from 125 m and 145 m at new moon. The calculated total for full moon was 1.4× that for new moon and the calculated size-frequency curves differed considerably. Both differences were due to larger catches of 17- to 23-mm fish at full moon. Both these data and the CT-IK comparisons indicate that the IK missed some smaller fish in the upper layers at new moon. If these differences are real, they could in part account for the apparent lower numbers and percents of juveniles estimated in night series (see above).

There were substantial numbers of juveniles (<20 mm) in the June, July, and September series with few in December 1970 and practically none in March 1971. The percentages of mature females with developed ova (Table 2) were highest in March and June 1971 and significantly lower in December 1970. These suggest that spawning occurs principally in spring and summer and that the juveniles have reached trawlable size within a few months.

Bolinichthys supralateralis

No *B. supralateralis* over 53 mm long were taken above the day depth range. Out of 15 such individuals, only 3 were caught during deep night tows. These could well have been contaminants and do not clearly confirm that the larger individuals do not migrate. However, out of 50 smaller fish caught at night, 10 were caught in tows within the day depth range suggesting that all sizes may not regularly migrate. In the upper layers at night, fish less than 20 mm occurred between 100 and 200 m, but only two between 20 and 30 mm and none over 30 mm were caught above 200 m. All sizes appeared to occur throughout the day depth range.

The pooled IK size-frequency data indicated that *B. supralateralis* spawns principally in late summer and fall and that it may take at least 2 years to reach maturity. There were distinct, well-separated size classes in all but the March 1971 series where only 11 fish were caught. Small fish, 12-20 mm long, were most abundant and made up the majority of the catch in September and December 1970. It appeared that this group was represented by 24- to 35-mm individuals in June 1971. A second year class was suggested by size classes present only in the December 1970 and June 1971 series (41-53 mm and 47-59 mm, respectively). A few fish larger than 60 mm were caught in all series and may represent a third year class. The only female with developed ova was 88 mm long, almost the largest specimen taken. It is likely that such large individuals avoid the trawl in addition to being rather rare.

Ceratoscopelus warmingi

The smallest *C. warmingi* regularly collected in the trawl do not appear to regularly migrate. At night, individuals 15-19 mm long were caught both between 20 and 100 m and at 600-700 m. In June 1971, when these sizes were most abundant, about two-thirds of the juveniles remained at depth. There was no indication that larger fish did not regularly migrate.

Within both day and night depth ranges the size-frequency curves differed significantly. Except during June 1971, at night few fish over 40 mm were caught above 50 m and few smaller individuals were caught below 75 m. In the June 1971 series, however, large numbers of 15- to 19-mm fish were caught down to 140 m, throughout most of the night range. During the day, few individuals over 20 mm occurred at 600-700 m, and larger individuals occurred principally below 750-800 m.

At night the percentage of females among mature *C. warmingi* tended to decrease with depth. In March 1971, when large numbers of mature fish were caught at several depths, 89% of the mature fish from 25 to 30 m were females. At 50 and 80 m the value was 64%, significantly lower. The value at 95 and 100 m was 33%, and at 120 m was 31%. Both were significantly lower than the values from shallower tows. Similar, but nonsignificant, trends were present in the September and December 1970 series. The only day series where sufficient numbers of mature fish were collected at several depths was in December 1970; there were no trends or significant differences in percentages of females.

Comparison of day and night series was possible only for the June 1971 series due to poor timing of the night samples with respect to moon phase in September and December 1970 and inadequate coverage in March 1971. Both the calculated totals and size-frequency curves for June 1971 agreed quite closely. Since about 85% of the fish in this series were <20 mm, any differences for larger fish would be difficult to detect, but the other series showed no obvious indications of differential day-night avoidance.

The CT caught only 4× as many *C. warmingi* as the IK at 25 m, but outfished the IK by factors of 12-14× between 50 and 100 m. The calculated CT total was 7.4× the IK total; when only fish over 25 mm were included, the factor was 8.3. The size-frequency curves were similar at 25 m but differed significantly for the deeper tows, the CT catching larger proportions of larger individuals. The calculated curves differed similarly, even when only fish over 25 mm were included. Apparently, some of the smaller fish passed through the CT meshes, thus accounting for the differences at 25 m where these fish were more abundant, but the CT appeared to sample the larger fishes, particularly those over 35 mm, better than the IK.

At new moon in September 1971, the depth of peak abundance was at 45 m, and the majority of the population was between 15 and 100 m. During full moon, the peak depth was at 130 m, and the population was mostly between 100 and 170 m. The calculated total for new moon was about twice that for full moon, and the new moon tows caught slightly larger proportions of fish over 35 mm.

The calculated totals indicated that *C. warmingi* was present in comparable numbers in December 1970, March 1971, and June 1971 and much less abundant in September 1970, but the calculated size-frequency curves differed greatly (Figure 11). In June 1971, the population was about 90% juveniles (14-17 mm), and in December 1970, about 60% were over 40 mm with few under 20 mm. In March 1971, 70% of the juveniles were 20-40 mm, and in September 1970, most were either under 25 mm or over 45 mm. Changes in the numbers of juveniles accounted for most of the changes in abundance,

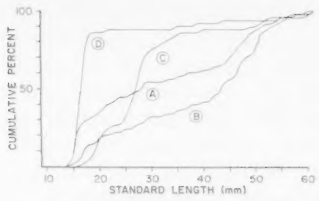

FIGURE 11.—Cumulative size-frequency curves of *Ceratoscopelus warmingi* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

but adults were definitely most abundant in December 1970 and almost absent in June 1971.

The large numbers of immature fish in March 1971 (particularly, a peak at 25-30 mm) suggest that some recruitment had taken place between December and March. The size composition of the population in June 1971 indicated a springtime spawning also. The percentage of ripe females was highest in June 1971, but none of the differences between series were significant. It appears that *C. warmingi* spawns over a long season, but principally during the first half of the year, and that there are either peaks within this season or marked fluctuations in larval and juvenile mortality.

Notoscopelus caudispinosus

N. caudispinosus was captured very rarely, but several fish, 20-25 mm, caught in March and June 1971 suggest that it may spawn in this area or nearby. It is possible that the larger individuals avoid both the CT and IK and are more abundant than the collections indicate.

DISCUSSION

Rare species

The majority of the species collected were rather rare. Only 19 species were present in moderate to high abundance and showed strong evidence of spawning in the area. A few of the rarer species appear to have primary centers of abundance elsewhere. The single *Diaphus theta* collected was certainly an expatriate from North Pacific transitional waters (Paxton, 1967), and four species are restricted to nearshore waters

(*Benthosema fibulatum*, *Diaphus adenomus*, *D. chrysorhynchus*, and *Lampadena urolampa*). *Diogenichthys atlanticus* and *Diaphus fragilis* are more abundant in Equatorial Pacific waters (Hartmann, 1971). The principal range of *Lampanyctus tenuiformis* is not clearly known.

Nineteen of the rarer species—*Protomyctophum beckeri*, *Myctophum* spp., *Loweina* spp., *Centrobranchus* spp., *Diaphus bertelseni*, *D. metopoclampus*, *D. "glandulifer,"* *Lampadena luminosa*, *L. anomala*, *Taaningichthys* spp., *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—appear to be typical of central or equatorial-central waters but are nowhere commonly collected (Bekker, 1966; Nafpaktitis, 1968; Nafpaktitis and Nafpaktitis, 1969; Gibbs et al., 1971; Wisner, 1971; Davey, 1972). Five of these species—*Myctophum selenoides*, *Diaphus* "glandulifer," *Lampadena luminosa*, *Taaningichthys minimus*, and *Bolinichthys supralateralis*—appear to spawn in the study area. *Lampadena urophaos*, although designated as a transitional water mass species by Paxton (1967), would appear to belong with the above group. It appears to spawn in this area, and a rough comparison of the present study's and Paxton's catch per effort indicates that it is more abundant near Hawaii.

Avoidance

Although it was not possible to set confidence limits for the calculated totals and size-frequency curves, in most species the differences between day and night totals were not large enough to suggest that there was substantially greater avoidance at either time. The exceptions, *Lampanyctus steinbecki* and the *Hygophum* spp., were sampled better during the day than at new moon at night. They also apparently avoid the IK better at new moon than at full and may be sampled equally well by night tows at full moon and day tows.

These results contrast with those of Pearcy and Laurs (1966) off Oregon. They noted substantial differences in day-night avoidance among mesopelagic fishes. The differences were in the opposite direction of the few noted in this study; most of their species avoided the net better during the day. Pearcy and Laurs used a 6-ft IK, and perhaps the larger trawl used in the present study sampled fishes relatively better during the day.

The IK-CT comparisons show that, as Harrisson (1967) and others have suggested, no single net will adequately sample all species. The IK gave higher estimates of overall abundance than the CT for many species analyzed, but greatly underestimated the abundance of two species, *Symbolophorus evermanni* and *Lampanyctus nobilis*. The CT sampled the *Hygophum* species better at night during new moon, but the IK probably samples them as well or better during the day or during full moon at night. Even allowing for escapement of small fishes through the CT meshes, the CT caught higher proportions of larger fishes of some species, e.g., *Ceratoscopelus warmingi* and *Lampanyctus steinbecki*. Neither net effectively sampled the mature sizes of *Lampanyctus nobilis*, *Lampadena luminosa*, and *Bolinichthys supralateralis*.

There was evidence for some species that one trawl sampled better at some depths only. The IK appeared to sample *Hygophum reinhardti* and *Bolinichthys longipes* as well or better than the CT at the deeper end of their night depth ranges, but the CT sampled as well or better at the shallower end. For *Diaphus schmidti* and *Diaphus* species A, the CT appeared to underestimate abundance at the shallower end of the depth range and caught relatively more fish at the deeper end. Obviously, more data are needed since one or two very high or low catches could have produced these results.

Harrisson (1967) using only roughly comparable pairs of samples, suggested that a larger otter-type trawl towed at 1 m/sec caught more larger fish than an IK towed at 1.5 m/sec. Aron and Collard (1969), however, have shown that towing speed had an important effect on an IK's estimates of abundance and size composition for one of the more abundant species collected in their study. Kuba (1970) found that in the Equatorial Pacific, the IK at 2 m/sec sampled most species' abundance and size composition as well or better than the CT at 1.5 m/sec. It would appear that the higher speed used for the IK tows in this study gave

a greater overall advantage than the increased "stealth" of the larger CT.

The full-new moon series indicated that most species occurred deeper at full moon and that several avoided the trawl better at full moon. The *Hygophum* species appeared to do just the opposite. The changes suggest that it is best overall to sample the upper 200 m at new moon only. A mixed sampling program can result in some populations being sampled twice and the depth range and abundance overestimated, or most of the population being missed and abundance underestimated.

Most species appeared to occur 50-75 m deeper at full moon. Data presented by Clarke (1970), however, indicate that in clearest ocean water, the depths of isolumes at full moon are about 200 m greater than at new moon. This suggests that the fishes occurred at higher light levels at full moon and may explain the increased avoidance noted then. The data of Blaxter and Currie (1967) indicate that this is possible. They observed that the depth of a sonic scattering layer was depressed by artificial light but to a light level about 10 times brighter than that at which the layer normally occurred.

Intraspecific Variations in Migration

Most myctophid larvae appear to occur in the upper layers (Ahlstrom, 1959). Whether they descend just prior to or just after metamorphosis is not known, but at least some species do not begin to undertake regular, extensive diurnal migrations immediately after metamorphosis. The data indicate that the recently metamorphosed juveniles of *Benthosema suborbitale*, *Lampanyctus niger*, *L. nobilis*, and *Ceratoscopelus warmingi*, and possibly *Hygophum proximum*, *Symbolophorus evermanni*, and *Bolinichthys longipes*, do not regularly migrate. More thorough sampling of the deeper layers at night with opening-closing devices may show this to be a general feature of myctophids.

Nafpaktitis (1968) has suggested that gravid females of some myctophids do not migrate. No evidence of this was found. The larger males of *Diaphus brachycephalus* and the larger individuals of *Bolinichthys supralateralis* appeared to remain at depth both day and night, but in both cases data were too few to be certain. In the latter species, there was no clear relation to maturity or reproductive condition. Most of the "nonmigrating" *B. supralateralis* were immature.

Large fractions of the populations of three species, *Notolychnus valdiviae*, *Lampanyctus niger*, and *Triphoturus nigrescens*, appeared to remain at the day depth during the night on some occasions. It is unlikely that the deep night catches were due to contamination, i.e., encountering aggregations in the upper layers on the way up or down. The numbers caught at depth during the December 1970 series were in all cases considerably larger than those caught in short oblique tows made during the same series. Also it seems unlikely that patches would be encountered only by tows made to the same depths where the species were found during the day. Finally, the day and night calculated totals and size frequencies agreed well for all three species in December. If the deep night catches had been contaminants, the night totals would have been much larger than those for the day.

There were no obvious differences between the migrating and nonmigrating fractions of the populations. The nonmigrating fraction of *Lampanyctus niger* tended to be smaller and that of *Notolychnus valdiviae*, larger in September 1970, but there was considerable overlap between both fractions of the populations in both cases. For *Triphoturus nigrescens* and *N. valdiviae* in December 1970, both fractions of the populations were nearly identical in size composition. Thus the difference in behavior was not entirely a function of size. There was no case where shallow and deep night samples differed in sex ratio or percentage of ripe females. The number of specimens involved was rather large in all cases, so it is doubtful that more data would produce clearer trends or any explanation related to the parameters measured here.

Most species showed significant differences in size composition with depth. *Symbolophorus evermanni* was the only species present in abundance for which all sizes appeared to occur throughout the depth range. In the great

majority of species, the juveniles tended to occur shallower than adults. The trend was more obvious in the night samples due to closer sample spacing, but probably holds for the daytime depth distribution in most cases. *Hygophum proximum* and *H. reinhardti* were anomalous in that at night during new moon the adults tended to occur shallower than the juveniles.

The changes in size composition with depth may be an artifact caused by larger fish avoiding the trawl better at lesser better-lighted depths. However, many small species such as *Benthosema suborbitale*, *Diaphus schmidti*, *Triphoturus nigrescens*, and *Notolychnus valdiviae* are unlikely to avoid the trawl even as adults, and the trends with depth were as evident with these species as with the larger species. Also the same trends were evident from CT data for species which the CT appeared to sample larger individuals relatively better. Furthermore, avoidance by larger fish would only partly explain the changes noted for many species, i.e., the smaller fish were absolutely less abundant with depth.

The ecological significance of the trends in size with depth is not clear. The juveniles are removed to some extent from predation by adults, but this is of doubtful significance since other predators are probably more important. Possibly the smaller fish are less visible to predators than are the adults in the better-lighted shallow layers. In those species where adults occur farther below the juveniles in the day than at night, it may be related simply to the juveniles being unable to make longer migrations. This pattern could be related to distribution of food. It is quite likely that juveniles require greater concentrations and smaller average particle size of food than adults, and optimal conditions for juveniles may occur shallower than for adults.

Sex Ratios

Sex ratios of mature and juvenile fish of several species are compared in Table 3. The difference is significant for only one species, *Diaphus schmidti*, and in that case, the ratios did not differ significantly when data for mature fish from a single sample with a very large proportion of females was not included. For most species there was a tendency for higher proportions of females among immatures, but the figures are suspect in the sense that the data were not properly weighted to account for possible trends with depth or season. Legand and Rivaton (1970) have noted opposite trends in sex ratio with size for three species of myctophids. (However, their criteria for separating "larger" from "smaller" fish is not entirely unbiased and the proportions given for one species, *Benthosema simile*, do not differ significantly.)

TABLE 3.—Proportions of females among juveniles and mature fish for nine species of myctophids. Number of specimens examined is given in parentheses.

Species	Juveniles		Adults	
Benthosema suborbitale	0.48	(54)	0.51	(230)
Hygophum proximum	.58	(67)	.46	(192)
Diaphus schmidti	.43	(56)	.62	(127)
Notolychnus valdiviae	.50	(70)	.45	(402)
Lampanyctus niger	.65	(55)	.57	(456)
Lampanyctus steinbecki	.65	(48)	.51	(535)
Triphoturus nigrescens	.59	(49)	.48	(452)
Bolinichthys longipes	.58	(66)	.48	(239)
Ceratoscopelus warmingi	.59	(96)	.58	(456)

Given that there may be trends in sex ratio with size, recognition of trends with depth or season was made difficult because there were only a few series where sufficient numbers of similar-sized fish were captured at several depths or several seasons. Thus, significant trends in sex ratio with depth were observed for mature fish of only a few species. Quite possibly, more data would show that these trends are the rule rather than the exception. When data were pooled for all mature fish examined from each series (Table 4), some significant differences in sex ratio were observed. In most cases one series showed significantly higher or lower percentage of females than the rest with no suggestion of seasonal trends. Again, however, differences in depth composition of the samples or size composition of the fishes pooled for a series may have either obscured trends or have been responsible for the few significant differences observed.

Seasonal Trends

In considering seasonal trends, it was assumed

TABLE 4.—Proportion of females among total mature fish at different seasons for 10 species of myctophids. Total number examined is given in parentheses.

Species	September		December		March		June	
Benthosema suborbitale	0.51	(35)	0.59	(105)	0.42	(90)	—	
Hygophum proximum	.56	(66)	.32	(22)	.34	(64)	0.55	(40)
Diaphus schmidti	.36	(22)	—		.71	(100)	.52	(21)
Diaphus sp. A	.57	(81)	—		.32	(28)	.52	(27)
Notolychnus valdiviae	.48	(133)	.49	(141)	.23	(48)	.48	(80)
Lampanyctus niger	.58	(86)	.52	(183)	.58	(119)	.69	(68)
Lampanyctus steinbecki	.42	(99)	.55	(40)	.63	(163)	.52	(233)
Triphoturus nigrescens	.52	(25)	.45	(314)	.48	(85)	.80	(45)
Bolinichthys longipes	.41	(29)	.43	(40)	.50	(139)	.55	(31)
Ceratoscopelus warmingi	.73	(15)	.59	(29)	.32	(41)	.46	(26)

that the same or equivalent populations were sampled on each cruise. Possible changes due to horizontal advective transport were ignored. Advection rates, especially for organisms which spend one-half of their time below the surface layers, and horizontal gradients in the parameters measured—abundance, size composition, etc.—are probably low. It seems unlikely that populations which had been subjected to greatly different environmental conditions were advected into the study during the periods between cruises.

The most likely possibility of change due to advection would be related to seasonal north-south shifts of water masses. Near Hawaii in the upper layers, water transitional between North Pacific Central and North Pacific Equatorial displaces North Pacific Central water during the summer. This shift is known to affect the abundance of skipjack tuna (Seckel, 1969).

The absence of marked changes in species composition and relative abundance of the myctophid fauna suggest that north-south shifts of water masses did not, during the study period, markedly affect populations. Two examples illustrate this particularly well. *Diaphus schmidti*, a species of myctophid which apparently does not occur much further south than Hawaii, was consistently taken here in abundance, while a very similar congener, *D. garmanni*, which is very abundant from at least lat. 12°30′N and further south (Hartmann, 1971), was never taken. Two species, *Diogenichthys atlanticus* and *Diaphus fragilis*, which are very abundant in equatorial waters (Hartmann, 1971), were taken consistently but never in great numbers near Hawaii.

Most species that showed seasonal changes in size composition appeared to reach maturity in about 1 year. The larger species—*Lampadena* spp., *Lampanyctus nobilis*, *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—probably take longer. In many species the adults nearly or completely disappeared at about the same time that juveniles became most abundant suggesting that few individuals live longer than 1 year.

The ages at maturity and life spans of colder water species of myctophids, e.g., *Benthosema glaciale* (Halliday, 1970), *Stenobranchus leucopsaurus* (Smoker and Pearcy, 1970), are considerably greater than those suggested here for tropical species. Murphy (1968) has presented data on epipelagic clupeoid fishes which show a marked decrease in age at maturity, the number of reproductions, and life span related to year-to-year variability in spawning success. He suggests that the latter is directly related to year-to-year variability in the physical environment. It is not unreasonable that the same trend exists for a mesopelagic family that occurs in both variable high-latitude waters and in the more stable tropical open ocean.

Most species appear to spawn predominately in the spring or summer. Primary production measurements taken by S. A. Cattell near Hawaii during 1969-70 indicate that primary production and productivity index are much higher during March-June than the period from October to January. Zooplankton production probably lags behind the peaks in primary production only slightly. Assuming that this seasonal pattern recurred during the present study, the period of principal spawning for most myctophid species appears to be timed

with respect to the seasonal peak in production of food.

In many of the abundant species, the seasonal changes in abundance and size composition were quite pronounced. When these were combined with size-dependent differences in migration habits, the depth-abundance profile also changed with season. Consequently, samples from only one period may give a misleading picture of vertical distribution and abundance. This would be particularly true in the tropics where, as opposed to longer-lived species at higher latitudes, several different size classes are not often present in abundance at all seasons.

Interspecific Relations

Many species of myctophids, including some congeners that are very similar morphologically, occur together in the water column yet must be ecologically segregated. From this study it is possible to examine several relevant factors: depth distribution, size range, and size changes with depth and season. Owing to better data for some of these aspects for the nighttime, only night distributions will be considered. There are, however, some data (Backus et al., 1968 Barham, 1970) that suggest that myctophids are rather inactive during the day and that interspecific patterns at night are probably more meaningful ecologically.

In Figure 12, depth-size patterns are diagrammed for 16 of the 19 most abundant species. For each species, a straight line is drawn connecting the size-depth coordinate for smallest size-shallowest depth with that for largest size-deepest depth. *Symbolophorus evermanni*, which showed no trend, and the *Hygophus* species, which will be discussed separately, have been omitted. Extremes of depth of capture and size range have been ignored; consequently, the ranges shown in Figure 12 are, in some cases, narrower than those given in Table 1. The straight lines are of course only a rough approximation to the actual patterns of size and depth; it is realized that more data would probably result in polygons for each species.

The species can roughly be separated into three groups. The first group includes eight species whose young occur principally at about 25 m and the adults between 75 and 125 m, depending on size. In the second group of three species, the pattern is similar except that the young occur principally at 80-100 m and the adults down to 150-250 m, again depending on size. The third group includes four species with sharper gradients in size with depth where juveniles occur around 50 m and larger fish are mostly between 150 and 200 m. Two of the rarer species, *Myctophum selenoides* and *Lampadena luminosa*, appear to have patterns like those of the third group. *Diaphus anderseni* has a depth-size pattern different from any of those illustrated, but two rarer species, *Taaningichthys minimus* and *Bolinichthys supralateralis*, appear to have similar patterns.

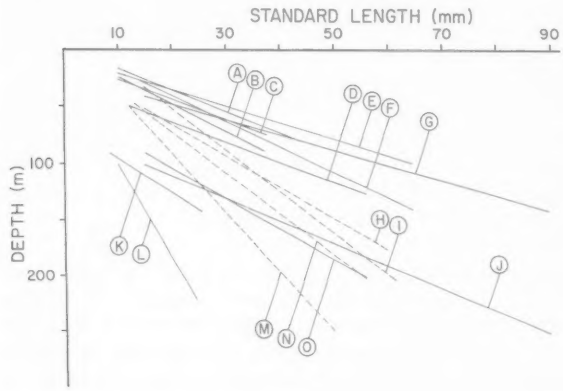

FIGURE 12.—Depth-size profiles (see text) in the upper 250 m at night for 16 species of myctophids: *Diaphus schmidti* (A), *Diaphus* sp. A (B), *Benthosema suborbitale* and *Triphoturus nigrescens* (C), *Bolinichthys longipes* (D), *Diaphus elucens* (E), *Ceratoscopelus warmingi* (F), *Lampanyctus nobilis* (G), *Diaphus rolfbolini* (H), *Diaphus* sp. B (I), *Lampanyctus niger* (J), *Notolychnus valdiviae* (K), *Diaphus anderseni* (L), *Lobianchia gemellari* (M), *Diaphus brachycephalus* (N), and *Lampanyctus steinbecki* (O).

Within the first two groups, similar sizes of the species tend to occur at similar depths. The depth-size patterns of four species in the first group—*Benthosema suborbitale*, *Diaphus schmidti*, *D.* sp. A, and *Triphoturus nigrescens*—are nearly identical. Within the third group, the juveniles co-occur with similar-sized individuals of the first group and the adults with larger fish of the second group.

Judging from the seasons of peak juvenile abundance (Table 1) most species in group one have similar reproductive cycles; large numbers of juveniles were present in the June or July samples. Juveniles were present in substantial numbers also in September for *Diaphus schmidti*, *D.* sp. A, and *Bolinichthys longipes*. *D. elucens* showed a peak in September only. *Benthosema suborbitale* and *Ceratoscopelus warmingi* showed large numbers of juveniles also in March. In group two, *Notolychnus valdiviae* and the smallest *Lampanyctus steinbecki* co-occur in summer and fall. *L. niger*, in spite of its apparent later season of maximum recruitment, is recruited at a larger size and co-occurs with similar sized *L. steinbecki* over much of the year. Thus there is a good deal of overlap in time as well as depth and size range for these species.

In general, congeners and closely related species, except *Hygophum* spp., have different size-depth patterns at night. Within each of the above groups, there are few congeners, and the co-occurring congeners are rather dissimilar. The four species of group one whose patterns are closest are of three genera, and the two congeners, *Diaphus schmidti* and *D.* sp. A, are quite different morphologically. Similarly, in group two, the *Lampanyctus* spp. belong to different groups within the genus.

Taaningichthys minimus and *T. bathyphilus* differ in that only *T. minimus* migrates. *Bolinichthys longipes* and *B. supralateralis* differ not only in morphology, size, and depth distribution but also in overall abundance. The two most similar *Lampanyctus* species, *L. steinbecki* and *L. nobilis*, which were present in abundance, have different night depth ranges and different sizes at maturity. Among the *Diaphus* species, closely related or similar species-pairs are distinctly separated even though most species appear to have similar reproductive cycles with peak juvenile abundance in June or September and nearly the same day depths. *D. rolfbolini* and *D. elucens* have different depth distributions at night. *D.* sp. A and *D.* sp. B differ in depth distribution and also in size at maturity. The species-pair of *D. anderseni* and *D. brachycephalus* differs similarly.

The depth-size patterns of the different species suggest that closely related species differ in their responses to physical factors and that genera or groups within genera have different biological requirements. Strong gradients in temperature, salinity, and light exist in the upper 250 m, particularly for temperature and salinity between 100 and 250 m. These are the most obvious factors to explain the differences in patterns of closely related species. Within each group, however, similar-sized individuals of dissimilar species co-occur under identical physical conditions. For them to co-exist, it would seem that they must be specialized with respect to biological factors.

A likely hypothesis is that the species within a group have different food preferences. Morphological differences between species within the groups include many features probably related to finding or capturing food; relative size of the eye and gape and the number, spacing, and structure of gill rakers. Closely related species of different groups are often rather similar in these respects.

The behavior of the *Hygophum* species appeared to be different from that of the other myctophids. The change in size-depth pattern between new and full moon was unique. The juveniles of *H. proximum* co-occurred with those of species of the second group at new moon and occurred shallower than those of the first group at full moon. The changes in avoidance with moon phase were also unique and suggest that the *Hygophum* species responded to something besides the visual stimulus of the trawl.

The *Hygophum* species were the only two congeners that occurred together in even roughly comparable numbers [see Note (Added in press) under *Lampanyctus niger*]. The two species are quite similar morphologically. *H.*

reinhardti is more slender and has higher numbers of AO photophores, gill rakers, and fin rays. There was, however, a great deal of overlap in these features, and except for adult males separation of the two species was the most difficult of all species collected. (Indeed, comparison of Hawaiian specimens with *H. proximum* from equatorial waters, where *H. reinhardti* does not occur, indicated that the specimens from Hawaii were more like *H. reinhardti* in body proportions than those from the equator.)

The seeming overlap between these two species may be anomalous in that the study area is at the edge of the principal ranges of both. According to Bekker (1965), *H. proximum* occurs principally below lat. 20°N and *H. reinhardti* above lat. 20°N in the central part of the Pacific. Over most of their ranges these two species do not appear to occur together in abundance, and Hawaii appears to lie in the transition zone between one species and the other.

Importance in the Ecosystem

The estimated total numbers of individuals per 10^3 m^2 for nine abundant species is given in Table 5 for each of the quarterly series and the CT series in March 1971. These numbers are the calculated totals from the best series (day or night) from each quarter. Using the same weighting factors, the biomass per 10^3 m^2 for each species was calculated and is given in Table 6.

TABLE 5.—Estimated number (individuals/10^3 m^2) for nine species of myctophids at different seasons. Numbers are totals calculated (see text) from samples taken throughout the water column by Isaacs-Kidd trawl (IK) during September 1970, December 1970, March 1971, and June 1971 and by Cobb trawl (CT) during March 1971.

Species	Number/10^3 m^2				
	Sept.	Dec.	March		June
			IK	CT	
Benthosema suborbitale	23	40	26	20	14
Hygophum proximum	26	6	49	14	14
Diaphus schmidti	21	14	19	30	25
Notolychnus valdiviae	104	68	12	—	23
Lampanyctus niger	57	163	62	9	55
Lampanyctus steinbecki	82	75	43	16	81
Triphoturus nigrescens	45	248	96	7	23
Bolinichthys longipes	58	23	44	24	13
Ceratoscopelus warmingi	55	176	196	153	155
Total	471	813	547	273	403

TABLE 6.—Estimated biomass (wet weight in g/10^3 m^2) for nine species of myctophids at different seasons. Figures were calculated by the same method as those in Table 5.

Species	g/10^3 m^2				
	Sept.	Dec.	March		June
			IK	CT	
Benthosema suborbitale	4	11	10	7	1
Hygophum proximum	19	2	29	11	2
Diaphus schmidti	4	3	10	17	4
Notolychnus valdiviae	6	5	1	—	2
Lampanyctus niger	59	244	102	18	37
Lampanyctus steinbecki	34	34	43	11	61
Triphoturus nigrescens	5	41	19	1	3
Bolinichthys longipes	13	5	30	20	8
Ceratoscopelus warmingi	56	221	103	130	40
Total	200	566	347	215	158

The figures are probably low for several reasons. Neither IK nor CT filtered with 100% efficiency; Pearcy and Laurs (1966) estimated that filtering efficiency was 85% for a 6-ft IK with coarser mesh than used here. There is a negative bias due to avoidance. Substantial avoidance of either the IK or CT was demonstrated for many species, and some likely avoided both. This probably affected the biomass estimates more since the larger fish are more likely to avoid the net. (The CT figures for *Lampanyctus niger* are deceptively low since substantial numbers were caught by IK below the deepest depth sampled by the CT.) For March 1971, the estimated total number is about 7% higher and that for biomass about 20% higher if CT estimates for *Hygophum reinhardti* and *Lampanyctus nobilis* are included and the higher of the two estimates (IK or CT) is used for the other species. It was not possible to estimate reliably numbers and biomass for the less abundant species. They amounted to about 10% of the total numbers caught by the four quarterly series and would probably increase the estimates of total numbers and biomass by a similar factor.

The low totals in June reflect the fact that for most species few adults were present and the juveniles of the next generation were not fully recruited to the population. Other differences were largely due to changes in one or two important species. The peak in total numbers in December was due principally to

high values for *Triphoturus nigrescens* and *Lampanyctus niger*, and the peak in total biomass then was caused mainly by the larger numbers of *L. niger*, a large species, and the fact that *Ceratoscopelus warmingi* had the highest percentage of adults at this time. Overall, *C. warmingi* and *L. niger* were clearly the dominant species with respect to both numbers and biomass.

The average number of myctophids per m^2 was about 0.55 and the average biomass was about 0.32 g/m^2. These figures are lower than those given by Pearcy and Laurs (1966) for total mesopelagic fishes in the upper 1,000 m off Oregon—1.5 individuals and 3.6 g/m^2 for the night tows. The total number of the three dominant myctophids off Oregon was about 0.78/m^2. Analyses of other fishes collected off Hawaii is not yet complete, but inclusion of other groups, particularly the hatchetfishes, *Cyclothone*, and larger stomiatoids would likely raise the average number and possibly the average biomass to values comparable to those of Pearcy and Laurs.

Preliminary analyses of the biomass of other groups of micronekton indicate that most of the biomass in the upper 250 m at night is in the form of vertically migrating groups which are not present during the day and that the myctophids dominate the fauna as a whole. The only other important group of vertically migrating fishes were the gonostomatids whose biomass, principally from *Gonostoma* spp., was about one-fourth that of the myctophids. The myctophid biomass was one to two times that of the caridean shrimps and about one to four times that of the larger euphausiids, *Thysanopoda* spp.

The biomass of epipelagic fishes and larval fishes over 10 mm was about one-sixth that of the myctophids. The figure for epipelagic fishes may be low due to higher concentrations very near the surface, where the sampling was inadequate, and possibly greater avoidance. In general, however, the data agree with Ahlstrom's (1969) conclusions, based on abundances of larval fishes, that vertically migrating, mesopelagic groups—principally myctophids and gonostomatids—dominate the open ocean fish fauna.

Conservatively, the average biomass of micronekton is at least three times that of the myctophids or about 1.0 g/m^2. Most myctophids appear to have a 1-year life cycle, and in many species, the population is nearly totally replaced by each new generation. The difference between the highest and lowest estimates of myctophid biomass is greater than the average value. Yearly production is then probably higher than the average standing crop. It is not unreasonable to assume that the dynamics of other groups of micronekton are similar and that micronekton production is about twice the average standing crop.

If, following Ryther (1969), it is assumed that ecological efficiency in the open ocean is about 10% for each trophic level and the organisms are about 10% carbon, then a production of 0.2 g C/m^2 by the micronekton would require production of 2 g $C/m^2/yr$ by the trophic level below. The yearly primary production in this area is about 50 g $C/m^2/yr$ (S. A. Cattell, pers. comm.) with about 5 g $C/m^2/yr$ available to the third trophic level and 0.5 g $C/m^2/yr$ to the fourth. For the rather conservative estimate of micronekton production to result, ecological efficiencies must be higher than 10% or the food chain in the open ocean must be shorter than generally assumed by Ryther (1969) and others, i.e., the micronekton must be consuming a large fraction of production by herbivores.

A final point concerns the fate of micronekton production; about 2 $g/m^2/yr$ must be consumed by higher carnivores. Studies of the feeding habits of such predators as tuna; dolphin, *Coryphaena*; and lancet fish, *Alepisaurus* (Gibbs and Collette, 1959; King and Iversen, 1962; Haedrich and Nielsen, 1966; Fourmanoir, 1971) indicate that these predators consume few vertically migrating forms such as myctophids or gonostomatids. Tuna and dolphin appear to eat mostly epipelagic forms. Unless the standing crop of epipelagic micronekton has been greatly underestimated here or its turnover rate is greater than that of vertically migrating forms, the "typical" predators of the open ocean are consuming only a fraction of the production by micronekton. In order to identify the principal energy pathways in the open

ocean, more work is needed on the food habits of poorly studied pelagic predators such as sharks, porpoises, gempylids, and squids. Further attempts, such as those of Forster (1971), to collect potential mesopelagic predators are also needed.

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 161:107-146.
1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest, Rep. 13:39-44.

ARON, W., AND S. COLLARD.
1969. A study of the influence of net speed on catch. Limnol. Oceanogr. 14:242-249.

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, D. L. SHORES, J. M. TEAL, A. S. WING, G. W. MEAD, AND W. D. CLARKE.
1968. Ceratoscopelus maderensis: peculiar sound-scattering layer identified with this myctophid fish. Science (Wash., D.C.) 160:991-993.

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the Sond cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BARHAM, E. G.
1970. Deep-sea fishes: Lethargy and vertical orientation. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 100-118. U.S. Gov. Print. Off., Wash., D.C.

BEKKER, V. E.
1965. Lanternfishes of the genus *Hygophum* (Myctophidae, Pisces), systematics and distribution. Akad. Nauk SSSR, Tr. Inst. Oceanol. 80:62-103. (Transl. no. 45, Natl. Mar. Fish. Serv., Syst. Cent., U.S. Natl. Mus.)
1966. Slendertailed luminescent anchovies (genera *Loweina*, *Tarletonbeania*, *Gonichthys* and *Centrobranchus*) of the Pacific and Indian Oceans. Systematics and distribution. *In* T. S. Rass (editor), Fishes of the Pacific and Indian Oceans biology and distribution, p. 10-78. (Translated by Israel Program Sci. Transl., 1966; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT 65-50120.) (Original 1964 in Akad. Nauk SSSR, Tr. Inst. Okeanol. 73:1-74.)

BLAXTER, J. H. S., AND R. I. CURRIE.
1967. The effect of artificial lights on acoustic scattering layers in the ocean. Symp. Zool. Soc. Lond. 19:1-14.

CLARKE, G. L.
1970. Light conditions in the sea in relation to the diurnal vertical migrations of animals. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 41-50. U.S. Gov. Print. Off., Wash., D.C.

DAVY, B.
1972. A review of the lanternfish genus *Taaningichthys* (family Myctophidae) with the description of a new species. Fish. Bull., U.S. 70:67-78.

FORSTER, G. R.
1971. Line-fishing on the continental slope. III. Mid-water fishing with vertical lines. J. Mar. Biol. Assoc. U.K. 51:73-77.

FOURMANOIR, P.
1971. Liste des espèces de poissons contenus dans les estomacs de thons jaunes, *Thunnus albacares* (Bonnaterre) 1788 et de thons blancs, *Thonnus alalunga* (Bonnaterre) 1788. Cah. O.R.S.T.O.M., Sér. Océanogr. 9:109-118.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1959. On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselus*. Bull. Mar. Sci. Gulf Caribb. 9:117-152.

GIBBS, R. H., JR., R. H. GOODYEAR, M. J. KEENE, AND D. W. BROWN.
1971. Biological studies of the Bermuda Ocean Acre. II. Vertical distribution and ecology of the lanternfishes (family Myctophidae). Rep. to U.S. Navy Underwater Syst. Cent., Smithsonian Inst., Wash., D.C., 141 p.

GORDON, D. C.
1970. Chemical and biological observations at Sta. Gollum, an oceanic station near Hawaii, January 1969 to June 1970. Rep. Hawaii Inst. Geophys., Univ. Hawaii, HIG-70-22, 44 p.
1971. Distribution of particulate organic carbon and nitrogen at an oceanic station in the central Pacific. Deep-Sea Res. 18:1127-1134.

HAEDRICH, R. L., AND J. G. NIELSEN.
1966. Fishes eaten by *Alepisaurus* (Pisces, Iniomi) in the southeastern Pacific Ocean. Deep-Sea Res. 13:909-919.

HALLIDAY, R. G.
1970. Growth and vertical distribution of the glacier lanternfish, *Benthosema glaciale*, in the northwest Atlantic. J. Fish. Res. Board Can. 27:105-116.

HARRISSON, C. M. H.
1967. On methods for sampling mesopelagic fishes. Symp. Zool. Soc. Lond. 19:71-126.

HARTMANN, A. R.
1971. Distribution of myctophid fishes across the equatorial current system in the Central Pacific. M.S. Thesis, Univ. Hawaii, Honolulu, 46 p.

HIGGINS, B. E.
1970. Juvenile tunas collected by midwater trawling in Hawaiian waters, July-September, 1967. Trans. Am. Fish. Soc. 99:60-69.

KING, J. E., AND R. T. B. IVERSON.
1962. Midwater trawling for forage organisms in the central Pacific, 1951-1956. U.S. Fish Wildl. Serv., Fish. Bull. 62:271-321.

KUBA, D. M.
1970. Sampling midwater fish using the ten-foot Isaacs-Kidd midwater trawl and the Cobb pelagic trawl. M.S. Thesis, Univ. Hawaii, Honolulu, 35 p.

LEGAND, M., AND J. RIVATON.
1970. Cycles biologiques des poissons mésopélagiques dans l'est de l'Océan Indien. Quatriéme *note*: Variations de répartition de 7 especes synthese des divers cycles décrits. Cah. O.R.S.T.O.M., Ser. Oceanogr. 8:59-79.

MURPHY, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391-403.

NAFPAKTITIS, B. G.
1968. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus*, in the North Atlantic. Dana Rep. 73, 131 p.

NAFPAKTITIS, B. G., AND M. NAFPAKTITIS.
1969. Lanternfishes (family Myctophidae) collected during Cruises 3 and 6 of the R/V Anton Bruun in the Indian Ocean. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 5, 79 p.

ODATE, S.
1966. Studies on the fishes of the family Myctophidae in the northeastern area of the Pacific coast of Japan. III. Determination of the age and growth of the susuki-hadaka lanternfish, *Myctophum affine* (Lutken). Bull. Tohoku Reg. Fish. Res. Lab. 26:35-43 (Fish. Res. Board Can. Transl. Ser. No. 850, 1967).

PAXTON, J. R.
1967. A distributional analysis for the lanternfishes (family Myctophidae) of the San Pedro Basin, California. Copeia 1967:422-440.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

RYTHER, J. H.
1969. Photosynthesis and fish production in the sea. Science (Wash., D.C.) 166:72-76.

SECKEL, G. R.
1969. Vertical sections of temperature and salinity in the trade wind zone of the Central North Pacific, February 1964 to June 1965. U.S. Fish Wildl. Serv., Circ. 323, 11 p.

SMOKER, W., AND W. G. PEARCY.
1970. Growth and reproduction of the lanternfish *Stenobranchus leucopsaurus*. J. Fish. Res. Board Can. 27:1265-1275.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Danville, Ill., 171 p.

WISNER, R. L.
1971. Descriptions of eight new species of myctophid fishes from the eastern Pacific Ocean. Copeia 1971:39-54.

APPENDIX TABLE 1.—Catches of myctophids in two series of four night tows each taken at 50 m and 100 m during July 1970. Only species with an average catch of 10/tow or more are considered separately. All tows were 2 hr at depth. The first three tows of each series were taken successively on the same night; the fourth was taken on the night immediately preceding (50 m) or following (100 m) the other three.

Species	Catch/tow			
	1	2	3	4
50-m series:				
Benthosema suborbitale	38	57	22	30
Diaphus schmidti	18	21	23	29
Diaphus sp. A	14	22	8	20
Triphoturus nigrescens	32	46	22	40
Bolinichthys longipes	24	49	40	38
Ceratoscopelus warmingi	237	226	120	214
Total myctophids in 50-m series	399	437	267	446
100-m series:				
Hygophum proximum	8	9	11	25
Notolychnus valdiviae	1	2	3	46
Lampanyctus steinbecki	7	30	47	73
Lampanyctus nobilis	0	12	20	64
Bolinichthys longipes	45	51	38	141
Ceratoscopelus warmingi	37	25	31	32
Total myctophids in 100-m series	127	164	184	447

APPENDIX TABLE 2.—Catches of several species of myctophids in short oblique tows and ranges of catches from horizontal tows. Given for each series are the range of catches considered positive in estimating lower limits of depth ranges (+'s) and the range considered negative and due to contamination (–'s). For the December 1970 and June 1971 series, the catches of short oblique tows are also given. Each of the four December tows made two cycles simulating descent and ascent of the trawl during horizontal tows, each of the three June tows made one descent and ascent.

Species	September 1970		December 1970					March 1971		June 1971					
					Oblique							Oblique			
	+	–	+	–	1	2	3	+	–	+	–	1	2	3	4
Benthosema suborbitale	14-68	0-9	10-114	0-4	1	3	1	12-84	0-5	6-24	0-4	0	0	0	0
Hygophum proximum	9-88	0-7	6-14	0-3	0	0	0	6-45	0-2	5-21	0-4	0	0	0	0
Diaphus schmidti	14-74	0-7	23-41	0-6	2	2	1	7-51	0-5	7-101	0-3	0	0	1	1
Diaphus sp. A	9-36	0-4	21	0-2	0	0	0	10-29	0-5	6-7	0-2	1	0	0	0
Notolychnus valdiviae	11-130	0-6	10-116	0-8	0	4	1	17-19	0-10	11-84	0-10	3	6	2	4
Lampanyctus niger	11-180	0-7	10-174	0-7	0	12	14	23-69	0-8	12-93	0-10	3	2	6	4
Lampanyctus steinbecki	18-311	2-13	15-77	0-12	7	9	6	12-58	0-5	9-90	0-6	6	0	0	0
Triphoturus nigrescens	11-108	0-7	27-288	0-13	11	32	17	15-116	0-8	5-34	0-4	1	0	0	0
Bolinichthys longipes	19-148	0-8	13-61	0-6	2	1	1	19-93	0-4	7-25	0-6	0	0	1	1
Ceratoscopelus warmingi	14-126	0-10	14-265	0-10	2	2	4	16-248	0-8	11-145	0-5	3	6	2	4

CELL TYPES, DIFFERENTIAL CELL COUNTS, AND BLOOD CELL MEASUREMENTS OF A PORTUGUESE SHARK, *CENTROSCYMNUS COELOLEPIS*, CAPTURED AT 700 FATHOMS

STUART W. SHERBURNE[1]

ABSTRACT

A Portuguese shark, *Centroscymnus coelolepis*, 620 mm (24.4 inches) in total length captured in a lobster trap 700 fm deep at Hudson Canyon in February 1971 had a mean erythrocyte size of 33.4 × 23.6 μ, which is larger than any previously recorded for the class Chondrichthyes. Both neutrophils and heterophils were found in the blood, whereas earlier reports describe only one or the other from the same elasmobranch.

Most sharks are shallowwater forms, with relatively few representatives from the deeper parts of the ocean. Bigelow and Schroeder (1948:494-499) reported that the Portuguese shark is strictly a deepwater shark, found chiefly in depths greater than 200 fm; it has been recorded down to 1,487 fm. The smallest recorded specimen is about 9 inches long, and the largest, about 44 inches. Off the North American coast it occurs mostly in temperatures of 5° to 6°C; off Portugal, between 4° and 11°C; and in the Mediterranean, at 12° to 13°C.

Few detailed studies have been made of either the blood or the blood-forming organs in elasmobranchs, probably because of difficulty in obtaining the necessary material (Saunders, 1966a). In this report I describe the cell types, differential cell counts, and measurements of both the erythrocytes and leukocytes in the blood of a Portuguese shark, *Centroscymnus coelolepis*. I report on this specimen because of its unusually large cell sizes in all cell categories. Cell measurements revealed erythrocytes larger than those in all but a few of the vertebrates, and the cells appear to be the largest reported for the class Chondrichthyes.

A search of the literature reveals no previous blood work has been reported on this species.

MATERIALS AND METHODS

The Portuguese shark examined for this report was a female, 620 mm (24.4 inches) in total length, and was captured in a lobster trap 700 fm deep at Hudson Canyon on 21 February 1971.

Smears were made with blood obtained by direct heart puncture of the live shark. A small incision was made over the heart area through which a heparinized capillary tube 75 × 1.1-1.2 mm was inserted into the heart and allowed to fill three-quarters full. A small drop of blood from the tube was placed on a microscope slide, the tube sealed with plastic clay and the smear made. Three capillary tubes were used to make four blood smears and the microhematocrit determination. The sealed tubes were centrifuged for 3 min at 11,000 rpm. Both a microcapillary reader and a millimeter rule were used in measuring the packed red cell volume, buffy coat, and plasma volumes.

The slides were air-dried and stained with Wright's and with Wright's and Giemsa's stains, and the staining times were varied.

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The best stain was obtained with 1½ min in Wright's followed by 20 min in Giemsa's stain; that slide was used in this study.

Cells were examined under oil immersion at 800 and 1200 power. Cells were measured at 800 power. Cell classification followed that of Saunders (1966a) for elasmobranch blood cells.

RESULTS AND DISCUSSION

This deepwater Portuguese shark had larger blood cell sizes, a lower hematocrit, and a different white cell differential count than those reported for other sharks.

Cell Differentials

Six classifications of cells were present: mature erythrocytes, immature erythrocytes, lymphocytes, heterophils, neutrophils, and thrombocytes. I found no monocytes, eosinophils, or basophils in the material I studied.

Mitotic division occurs in the circulating blood, for mitosis, in all stages, was present in a few cells in the blood smear (Figures 1, 2).

An erythrocyte differential count of a random sample of 100 red cells revealed that mature erythrocytes constituted 92% of the total, immatures 7%, and erythroblasts 1%.

The percentage of mature red cells agrees closely with Saunders' (1966a, b) findings for other elasmobranchs, but the white cell differential of this shark differed substantially from those of other elasmobranchs reported by Saunders. This shark had 73% lymphocytes, 22% thrombocytes, and 5% heterophils; whereas in 13 species of elasmobranchs Saunders found a maximum of 32% lymphocytes and 20-85% thrombocytes, and in 9 species, 3-54% heterophils. The large difference in lymphocyte frequency may be an individual characteristic of this specimen, for Saunders found a substantial difference between the white cell differentials of two adult specimens of sandbar shark, *Carcharhinus milberti*. Saunders also reported that either heterophils or neutrophils, but not both, are found in any given species of elasmobranch; however, I found a few neutrophils in addition to heterophils on close examination of the blood in this shark. Several were located at the end of the smear where a differential would not normally be made because of mechanical distortion of the cells; others were discovered in the area where a differential might be made, though the neutrophils could be easily overlooked because of their scarcity.

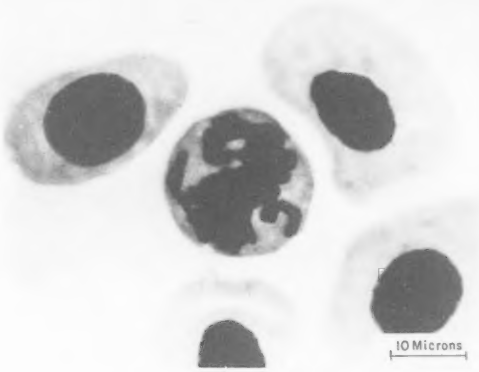

FIGURE 1.—Mitosis-Prophase.

FIGURE 2.—Mitosis-Anaphase.

Table 1 lists the measurements of all cells described in this report.

Mature Erythrocytes

The mean size of the Portuguese shark mature erythrocytes (Figure 3) is the largest

TABLE 1.—Blood cell measurements in microns of a Portuguese shark, the mean ± standard deviation and range in parentheses.

Cell type	Number of cells measured	Cytosome		Nucleus	
		Length	Width	Length	Width
Mature erythrocyte	200	33.4 ± 2.5 (26.5 − 40.6)	23.6 ± 1.8 (18.7 − 28.1)	13.4 ± 0.7 (12.2 − 15.4)	10.2 ± 0.6 (9.1 − 11.7)
Immature erythrocyte	10	25.8 ± 2.2 (21.8 − 27.9)	16.4 ± 2.2 (14.0 − 20.1)	15.0 ± 0.7 (14.0 − 16.1)	12.8 ± 1.0 (10.9 − 14.0)
Erythroblast	1	28.1	17.5	18.7	15.9
Heterophil	10	23.8 ± 1.5 (22.3 − 25.0)	22.6 ± 1.3 (21.8 − 25.0)	10.8 ± 1.2 (9.4 − 12.5)	15.2 ± 1.5 (12.8 − 17.2)
Lymphocyte	10	17.8 ± 2.2 (15.6 − 20.3)	16.8 ± 1.2 (14.0 − 18.7)	16.2 ± 2.0 (14.0 − 19.5)	14.7 ± 1.1 (12.5 − 16.4)
Thrombocyte	20	23.4 ± 2.7 (18.7 − 28.0)	13.2 ± 1.6 (10.9 − 17.2)	16.6 ± 1.1 (14.5 − 18.7)	9.4 ± 1.0 (7.8 − 11.1)
Neutrophil	5	23.6 ± 1.2 (21.8 − 25.0)	23.2 ± 0.9 (21.8 − 24.2)	11.2 ± 1.3 (9.4 − 12.5)	18.9 ± 2.7 (15.6 − 21.7)

reported for the Chondrichthyes, including the rays, which characteristically possess larger cells than sharks. A comparison of some of the largest recorded erythrocyte dimensions for the Chondrichthyes (Altman and Dittmer, 1961) with the Portuguese shark is listed below.

Species	*Erythrocyte dimensions (Dry films)*
Portuguese shark, *Centroscymnus coelolepis*	33.4 × 23.6 μ
Electric ray, *Torpedo nobiliana*	29.8 × 23.1 μ
Little skate, *Raja erinacea*	24.3 × 13.9 μ
Spiny dogfish, *Squalus acanthias*	22.7 × 15.2 μ
Hammerhead shark, *Sphyrna zygaena*	15.2 × 11.2 μ

Immature Erythrocytes

One thousand erythrocytes were counted on the slide and 8.6% of the cells were immature. A few erythroblasts were seen, and measurements of a typical one are listed in Table 1. Immature erythrocytes are easily distinguished from the mature cells by their larger nucleus and smaller cytosome (Figure 3).

Heterophils

Heterophils stained clearly to show purplish nuclear material and eosinophilic rods. The heterophils are quite round and similar in size (Figure 4).

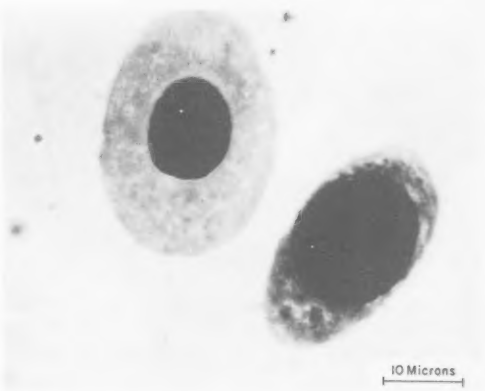

FIGURE 3.—Mature erythrocyte on the left, immature erythrocyte on the right.

Lymphocytes

Lymphocytes stained well with the purplish nucleus taking up most of the cell space. The cytoplasm stains a medium to deep blue and often shows blebs extending from the cell wall (Figure 5).

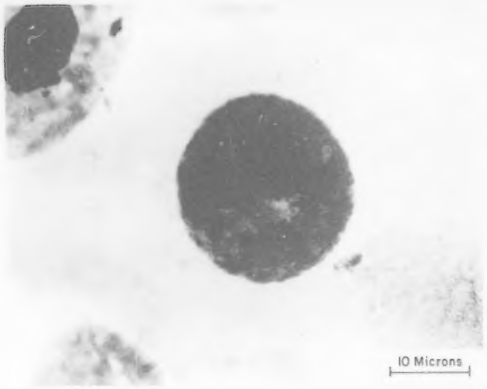

FIGURE 4.—Heterophil showing rod-shaped granules.

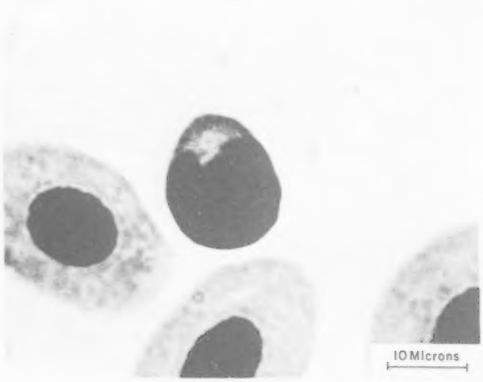

FIGURE 5.—Lymphocyte and three erythrocytes. This lymphocyte does not have blebs extending from the cell wall.

Thrombocytes

Thrombocytes, which are characteristically some of the smallest cells found in the peripheral circulation, were as large in this shark as many mature erythrocytes in other vertebrate species. The stained nucleus is ovoid with pink to red dotted cytoplasm. Since there is quite a range in the length of some of these cells due to fingerlike cytoplasmic projections, I measured 20 ovoid thrombocytes (Figure 6).

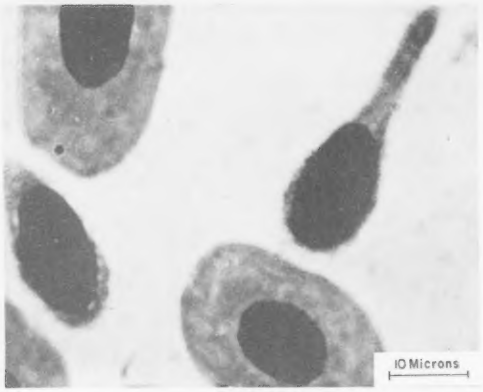

FIGURE 6.—Two thrombocytes, one with a fingerlike cytoplasmic projection.

Neutrophils

Neutrophils were scarce and were discovered only when the whole slide was studied in detail. They are within the same size range as the heterophils but are distinguished by the absence of eosinophilic rod-shaped granules and the colorless cytoplasm (Figures 7, 8).

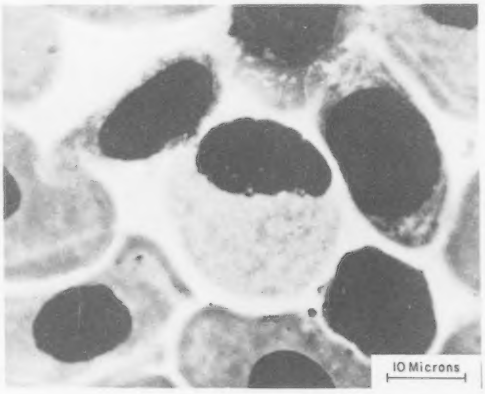

FIGURE 7.—Center: A neutrophil located at the end of the smear where other cells have been mechanically distorted. Clockwise: Immature erythrocyte, lymphocyte, mature erythrocyte, and thrombocyte.

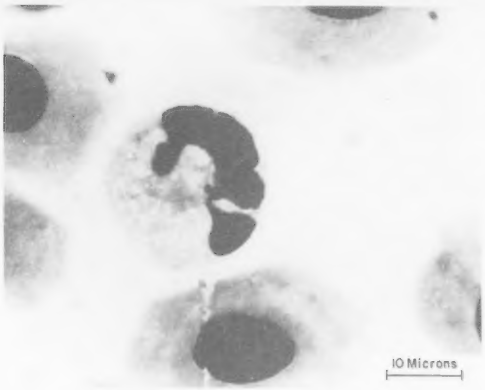

FIGURE 8.—Neutrophil showing a segmented nucleus.

Hematocrit

The packed cell volume of this deepwater shark was less than that reported for other sharks. In a 62 mm whole blood column, 52 mm was clear plasma, 2 mm buffy coat, and 8 mm packed erythrocytes. This was a 13% hematocrit compared with 17-32% from 11 wild dogfish (Burger, 1967) and 23.1% for the hammerhead shark (Altman and Dittmer, 1961).

The blood of the Portuguese shark examined showed no evidence of abnormality. There was no hemolysis in the plasma, and though the absolute cell sizes were larger than previously reported for other sharks, the staining and morphological characteristics of each cell category were typical of shark cells.

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LITERATURE CITED

ALTMAN, P. L., AND D. S. DITTMER.
1961. Blood and other body fluids. Fed. Am. Soc. Exp. Biol., Wash., D.C., p. 116-119.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic. Part One, p. 59-546. Sears Found. Mar. Res., Yale Univ., Mem. 1.

BURGER, W. J.
1967. Problems in the electrolyte economy of the spiny dogfish, *Squalus acanthias*. *In* P. W. Gilbert, R. F. Mathewson, and D. P. Rall (editors), Sharks, skates, and rays, p. 177-185. Johns Hopkins Press, Balt.

SAUNDERS, D. C.
1966a. Elasmobranch blood cells. Copeia 1966:348-351.
1966b. Differential blood cell counts of 121 species of marine fishes of Puerto Rico. Trans. Am. Microsc. Soc. 85:427-449.

MORPHOLOGICAL STUDY OF DIAGNOSTIC CHARACTERS IN WESTERN ATLANTIC *HEPOMADUS* (CRUSTACEA, DECAPODA, PENAEIDAE)

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The collections made during the expeditions of the *Oregon*, *Oregon II*, and the RV *John Elliott Pillsbury* almost tripled the number of specimens of *Hepomadus* previously recorded from the western Atlantic. The taxonomic status of the material has been assessed through a study of the external morphology and an investigation of variations of morphological, morphometric, and meristic characters. It is demonstrated that intermediates are present between extremes of variations and, consequently, all specimens are assigned to a single species, *Hepomadus tener* Smith.

The gap in our knowledge of the genus *Hepomadus* results from the great paucity of collections taken beyond the continental shelf of America. Although recent material caught in the course of the expeditions of the *Oregon*, *Oregon II*, and the RV *John Elliott Pillsbury*, in addition to five specimens taken by the *Albatross* in 1885 and 1886 which have not been reported, have almost tripled the number of specimens previously recorded from the western Atlantic (18), the total number of known specimens is only 51.

The purpose of this paper is to demonstrate that all specimens of *Hepomadus* that have been taken in the western Atlantic (including the Sargasso Sea, the Gulf of Mexico, and the Caribbean) belong to a single species, *Hepomadus tener* Smith, 1884. My study has drawn from the works of earlier investigators, and I have corroborated their observations on the great variation in many morphological and a few morphometric and meristic characters within this species. Additional material from a greater number and more widely distributed localities, however, have led me to conclude that features which have been suggested as probably useful in differentiating species of *Hepomadus* in the region are not valid. Similarly, all other characters analyzed here for the first time show a wide range of variation, with intermediate stages present between the extremes. One meristic and two morphological characters, however, have been found reliable for separating *H. tener* and *H. glacialis* Bate, 1881, which is known only from the western Pacific.

PRESENTATION OF DATA

The c.l. (carapace length—linear distance between orbital margin and midposterior margin of carapace) and r.l. (rostral length—linear distance from apex to orbital margin) are measured to the nearest 0.5 mm. The ratios presented in the tables are given to the nearest 0.05. Certain ratios are not given for every specimen because the rostrum is damaged in many of them, and, in some, the spine on the third pleonic somite is broken. The ocean depths have been recorded to the nearest meter. Finally, the scales accompanying the illustrations are in millimeters.

The following abbreviations are used for repositories of specimens: TAMU-Department of Oceanography, Texas A&M University; UMML-Institute of Marine Sciences, University of Miami; USNM-National Museum of Natural History, Smithsonian Institution; and YPM-Peabody Museum of Natural History, Yale University.

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HEPOMADUS TENER SMITH, 1884

Figures 1-10

Hepomadus tener Smith, 1884: 409, pl. 9 fig. 7-8. Holotype: ♂ USNM 5464. Type-locality: off mouth of Chesapeake Bay, 5,394m, 2 October 1883, *Albatross* stn 2099 (lat 37°12′20″N, long 69°30′W).-Smith, 1887:689, pl. 19, fig. 3-3a.-Bouvier, 1908: 57, pl. 1, fig. 5, pl. 13, fig. 1-12.-Burkenroad, 1936:86.-Ramadan, 1938:55.-Roberts and Pequegnat, 1970:43, fig. 3-2D.-Pequegnat and Roberts, 1971:9.

Hepomadus tener?.-Wood-Mason and Alcock, 1891:189.

Aristaeus (Hepomadus) tener?.-Alcock, 1901:42.

Hepomadus glacialis.-A. Milne Edwards and Bouvier, 1909:194, fig. 13-19, pl. 1, fig. 3. [Not *Hepomadus glacialis* Bate, 1881.]

Material

United States

New Jersey: 1 ♀, USNM, off Atlantic City, 2,601 m, 11 August 1885, *Albatross* stn 2563.

Delaware: 1 ♂, USNM, off mouth of Delaware Bay, 3,206 m, 18 September 1886, *Albatross* stn 2715. 1 ♀, USNM, off mouth of Delaware Bay, 2,983 m, 18 September 1886, *Albatross* stn 2716.

Virginia: 1 ♂, holotype, USNM 5464. 1 ♀, USNM, off mouth of Chesapeake Bay, 3,740 m, 10 September 1884, *Albatross* stn 2226. 1 ♂ 1 ♀, YPM, and 1 ♀, USNM, off Back Bay, 2,266 m, 24 October 1886, *Albatross* stn 2727.

North Carolina: 1 ♀, YPM, off Roanoke Island, 1,542 m, 11 November 1883, *Albatross* stn 2115.

Florida: 1 ♀, USNM, S of Santa Rosa Island, 1,463 m, 2 September 1970, *Oregon II* stn 11206.

Alabama: 1 ♂ 1 ♀, USNM, off Mobile Bay, 2,683 m, 2 March 1885, *Albatross* stn 2379. 2 ♀ USNM, off Mobile Bay, 1,555-1,829 m, 28 July 1962, *Oregon* stn 3664. 2 ♂ 1 ♀, USNM, off Mobile Bay, 1,646 m, 28 January 1970, *Oregon II* stn 10897.

Louisiana: 1 ♀, USNM, off Grand Terre Islands, 2,652 m, 28 July 1959, *Oregon* stn 2574.

Texas: 1 ♂, TAMU, off Padre Island, 1,399 m, August 1969, *Alaminos* stn 68-A-11-7.

Mexico

Tamaulipas: 1 ♂, TAMU, of Boca San Rafael, 3,384-3,493 m, November 1968, *Alaminos* stn 68-A-13-10. 1 ♂, TAMU, off Boca San Rafael, 3,658 m, March 1968, *Alaminos* stn 68-A-3-3B. 1 ♂ 1 ♀, TAMU, off Tampico, 1,774 m, August 1969, *Alaminos* stn 69-A-11-87.

Veracruz: 1 ♂, USNM, NE of Cabo Rojo, 896 m, 3 June 1970, *Oregon II* stn 10955. 3 ♂, USNM, SE of Cabo Rojo, 1,280 m, 3 June 1970, *Oregon II* stn 10957. 1 ♀, USNM, SE of Cabo Rojo, 1,097 m, 3 June 1970, *Oregon II* stn 10956.

Yucatan: 1 ♂, TAMU, NW of Progreso, 3,841 m, March 1968, *Alaminos* stn 68-A-3-5B.

Bahamas

1 ♂, YPM, Turks Island Passage, 1,646-1,728 m, 12 April 1927 *Pawnee* stn 54.

Haiti

1 ♂ 1 ♀, USNM, Gulf of Gonave, 3,109-3,493 m, 1 July 1970, *Pillsbury* stn 1180.

Tobago

1 ♂, USNM, NW of Charlotteville, 920-1,244 m, 2 July 1969, *Pillsbury* stn 847. 2 ♀, USNM, NE of Man of War Bay, 1,817-1,847 m, 1 July 1969, *Pillsbury* stn 844.

Western Caribbean

2 ♀, USNM, NW of Cayos Hobbies, 933 m, 24 October 1970, *Oregon II* stn 11217.

Panama

1 ♀, USNM, off Punta Manzanillo, 1,639 m, 25 March 1884, *Albatross* stn 2144.

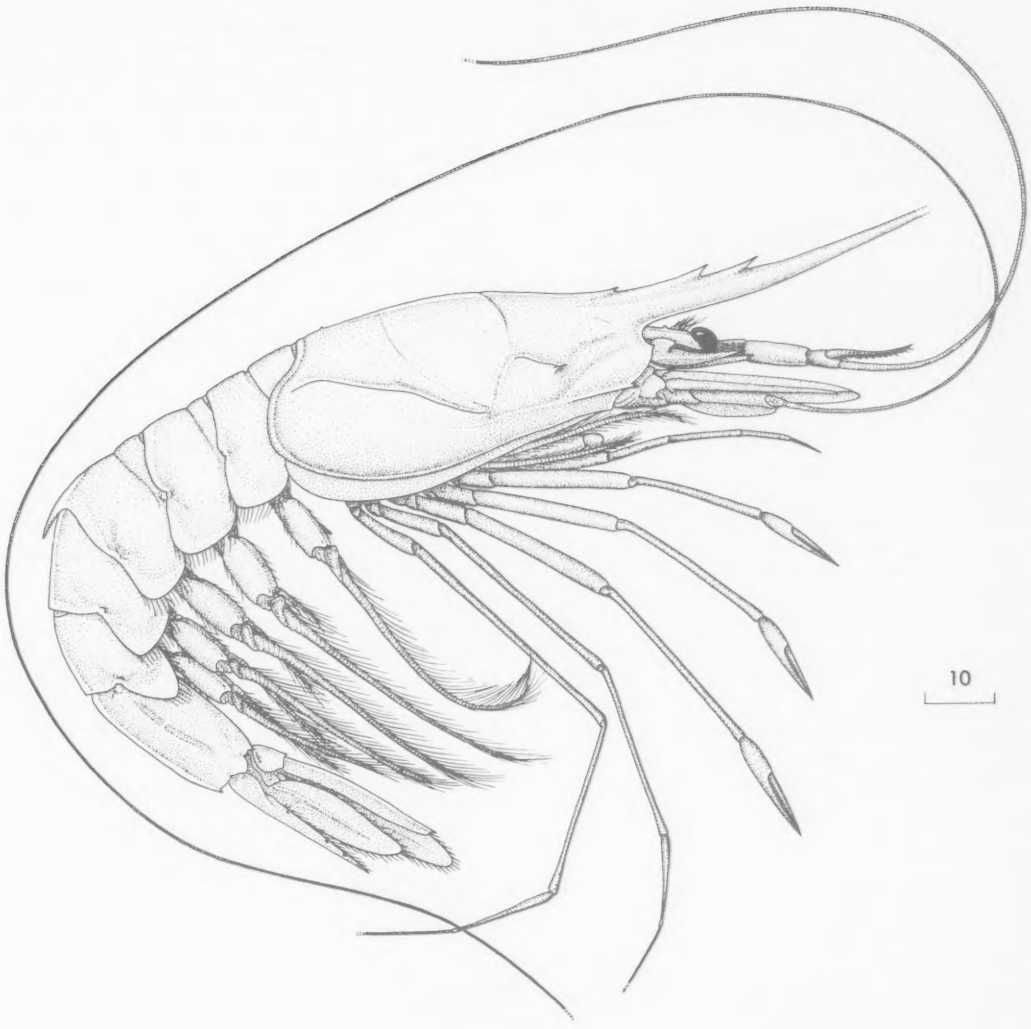

FIGURE 1.—*Hepomadus tener* Smith. Lateral view, ♀ 51 mm c.l., off Mobile Bay, Ala.

Colombia

1 ♂ 1 ♀, UMML, off Islas de San Bernardo, 1,271 m, 4 November 1970, *Oregon II* stn 11240. 3 ♂, USNM, off Isla de Barú, 1,097 m, 5 November 1970, *Oregon II* stn 11242. 1 ♀, USNM, off Puerto Colombia, 1,097 m, 8 November 1970, *Oregon II* stn 11245. 1 ♂ 1 ♀, TAMU, N of Cabo de la Aguja, 4,152 m, 24 July 1970, *Alaminos* stn 70-A-10-48. 1 ♀, USNM, NW of Península de la Guajira, 1,500 m, 27 July 1966, *Pillsbury* stn 454.

Description

Body slender and lacking setae (Figure 1). Dorsum of carapace almost straight or very slightly convex, convexity extending beyond postcervical sulcus (Figure 3A). Rostrum styliform, straight to slightly upturned in young (Figure 2), pronouncedly inclined dorsad in large individuals of both sexes; in young females and, apparently, in all males length of rostrum not exceeding 0.70 that of carapace, in larger females rostral length increasing with increasing size of shrimp to as much as 1.25 length of carapace, and surpassing antennular peduncle by about 0.3 of its own length. Rostral teeth 3, first tooth located slightly posterior to orbital margin, and rather far from second tooth; second and third teeth separated by interval varying from 0.3 to 0.6 of distance between first and second tooth. Postrostral carina (inconspicuous in young individuals) long, extending to about 0.8 length of carapace, and followed by rather minute dorsal tubercle, located near posterior margin; adrostral carina extending from orbital margin to near tip of rostrum, stronger and sharp basally. Orbital spine absent; antennal spine short, acute; branchiostegal spine produced and sharp; hepatic spine prominent. Cervical sulcus well marked, extending to middorsum of carapace, ending there at about 0.45 length of carapace from orbital margin; postcervical sulcus faint, concave except for almost straight, short, dorsal portion, ending at middorsum of carapace at 0.3 of carapace length from posterior margin; hepatic sulcus almost horizontal; orbitoantennal sulcus short and linear; branchiocardiac sulcus well marked, its length slightly more than half that of carapace, extending from near posterior margin of carapace to posterior end of hepatic sulcus.

Antennular peduncle length about 0.55 that of carapace; stylocerite produced distally into very slender, sharp spine, barely reaching base, or extending to midlength, of acute distolateral spine; first segment bearing minute ventromesial spine in young, occasionally spine persisting in animals of 24 mm c.l.; dorsal flagellum extremely long, about 4.5 times length of carapace, or 1.1 times total length of shrimp.

Scaphocerite 2.0 to 2.1 times as long as broad, and surpassing antennular peduncle by 0.1 to 0.2 of its own length; lateral rib produced distally into sharp spine overreached by lamella; antennal flagella incomplete in all specimens examined.

Labrum (Figure 4A, B) consisting of two

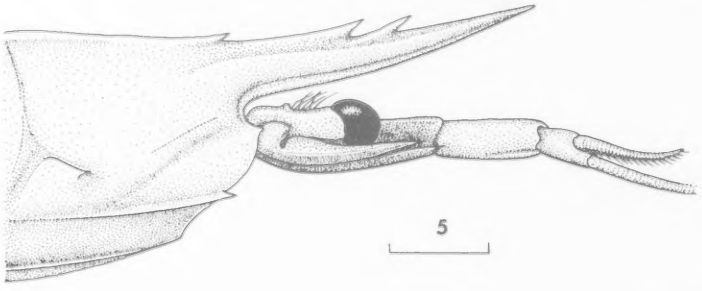

FIGURE 2.—*Hepomadus tener*. Anterior region, ♂ 28 mm c.l., mouth of Delaware Bay, Del.

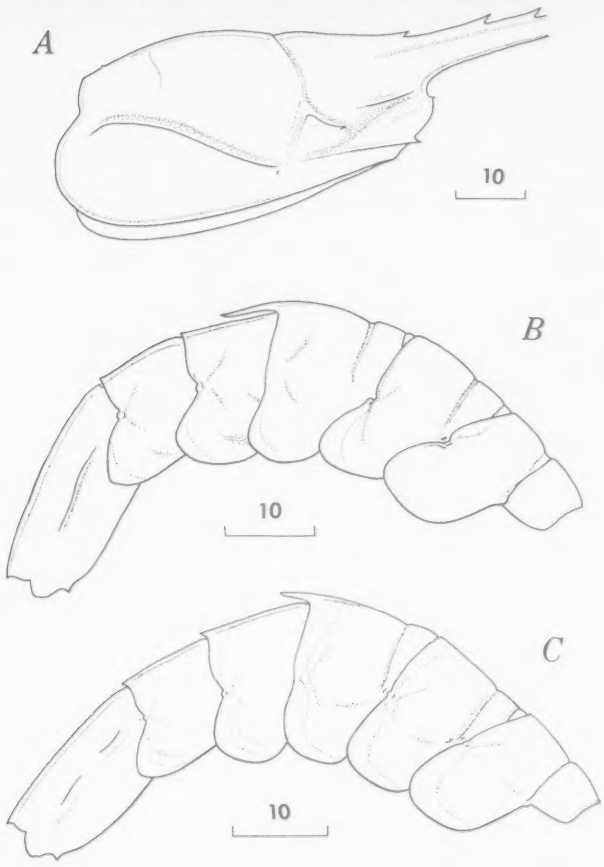

FIGURE 3.—*Hepomadus tener*. A. Lateral view of carapace, ♀ 52 mm c.l., off Back Bay, Va. B. Lateral view of abdomen, ♀ 51 mm c.l., off Atlantic City, N.J. C. Lateral view of abdomen, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz.

lightly sclerotized lobes: 1) anterodorsal lobe, subtriangular in outline, often bearing longitudinal, ventromedian carina, and ending anteriorly in vertical, apical ridge; lateral walls of lobe tapering from apical ridge posteriorly, and ending in caudally divergent, cornified, epistomal bars; and 2) posteroventral lobe, subtrapezoidal, delimited by lateral ribs projecting anteriorly as paired, small convexities on margin of lobe; posterior portions of ribs turning mesially but not meeting in midline.

Mandibular palp with proximal lobe of second segment ranging from blunt to acute. Second maxilla with endite of basis, "maxillary palp," bearing 2 to 4 strong and 1 to 4 weak setae [occasionally none according to A. Milne Edwards and Bouvier (1909) on a specimen identified as "*H. glacialis*"] on upper side of distolateral portion; and 2 to 5 strong and 1 to 4 weak setae, or none, on the lower side; in addition, 1 to 6 long, plumose, distal setae often present on upper side (Figure 5B, C). Number of setae on endite of right and left maxilla often different in same individual of this species as in holotype of *H. glacialis* (Figure 5D, E, left second maxilla). Exopod of first maxilliped with proximomesial border bearing 4 to 7 long, rigid setae.

Third maxilliped reaching base to distal end of third antennular segment, its dactyl with mesial side broadening abruptly at distal end

of proximal fourth forming excavation bearing strong setae on its proximal side, and tapering distally; first pereopod extending as far as, or very slightly beyond, third maxilliped; second pereopod reaching midlength of third antennular segment or surpassing it by tip of dactyl; third pereopod reaching distal end of antennular peduncle or exceeding it by almost 0.5 length of dactyl; fourth pereopod surpassing antennular peduncle by length of dactyl and 0.2 to 0.5 that of propodus; fifth pereopod overreaching antennular peduncle by length of dactyl and 0.5 or entire length of propodus—last two pairs of pereopods, especially their dactyls, slender. Ischium of third maxilliped bearing minute distomesial spine; merus of first and second pereopods with ventral distomesial spine movable, and rather stout. In females, coxae of last three pairs of pereopods produced mesially into plates covered with long setae and bearing anteriorly prominent, blunt tooth. In males, coxae of fifth pair of pereopods with large, obtuse to strongly acute tooth on anteromesial margin.

Abdomen with middorsal carina extending from about midlength of third somite through sixth, carina rounded on third, sharp from fourth posteriorly; posterodorsal margin of third somite bearing broad-based, prominent spine, its length 0.3 of, to equivalent to, distance between transverse sulcus and posterior margin of somite; posterodorsal margin of fourth and fifth somites varying from straight (Figure 1) to armed with well-developed, small spine (Figure 3B, C); sixth somite bearing small spine at posterior end of dorsal carina, paired posteroventral teeth, and two pairs of prominent lateral cicatrices; latter occasionally almost fused into one. Telson with four pairs of lateral minute, movable spines, posteriormost pair flanking very small terminal portion; median sulcus short, disappearing well anterior to terminal portion, mesial ramus of uropod longer than telson, and lateral ramus considerably overreaching mesial.

Petasma (Figure 6A, B) with median lobe tapering distolaterally from distal extremity of row of cincinuli (hooklike structures along mesial margin of median lobes of petasma that serve to interlock its two halves), and with elongate, subelliptical, sclerotized lapel on inner surface, extending along distomesial margin; lateral lobe very broad proximally, narrower and rounded distally; ventral costa with distal 0.4-0.5 of its length free from adjacent portion of ventrolateral lobule, and strongly curved

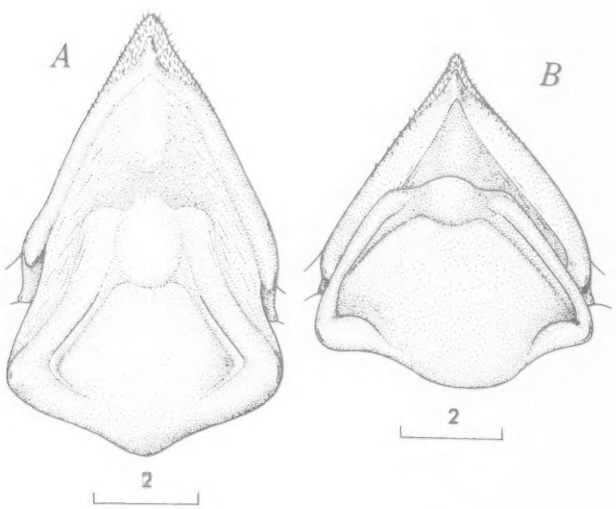

FIGURE 4.—*Hepomadus tener*. Ventral views of labra: A. ♀ 43.5 mm c.l., S of Santa Rosa Island, Fla. B. ♀ 44 mm c.l., off Back Bay, Va.

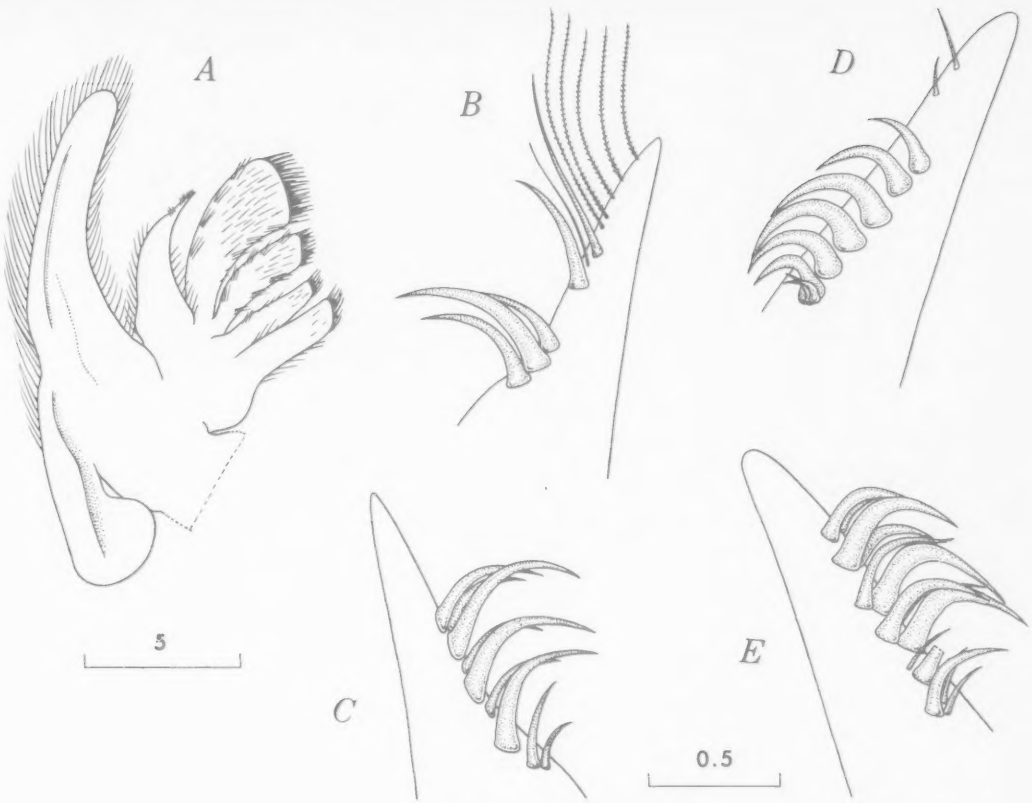

FIGURE 5.—*Hepomadus tener*. A. Dorsal view of left second maxilla, ♀ 51 mm c.l., off Atlantic City, N.J. B. Distalmost part of upper side of left endite, same specimen. C. Lower side of same endite. *Hepomadus glacialis* Bate, holotype, ♀ 65 mm c.l., near Yokohama, Japan. D. Distalmost part of upper side of endite of left second maxilla. E. Lower side of same endite.

laterally forming short, sinuous projection; articular sclerite produced proximomesially into strong, subrectangular spur situated immediately distal to large, platelike, mesially directed projection of basis of pleopod.

Appendix masculina (Figure 7A, B) broad, subfoliaceous, bearing long marginal setae on distal portion and secondary row along short rib, latter delimiting dorsal extremity of ventrally inclined distomesial portion of appendix. Appendix interna narrow, elongate, gently tapering distally to rounded extremity, and extending almost as far as, or somewhat beyond, appendix masculina.

Sternite XIII in males bearing lanceolate, median plate; sternites VIII through XII with high median ridge produced anteriorly into acute spine in males as well as in females.

Thelycum (Figure 8) with median plate on sternite XIII very elongate, reaching between midlength and anterior margin of sternite XII, roughly lanceolate, with gently undulate, or irregular, lateral margins, and rather abruptly tapering anteriorly forming usually obtuse, occasionally acute, triangular projection; sternite XIV weakly convex ventrally, convexity often embraced posteriorly by semicircular groove.

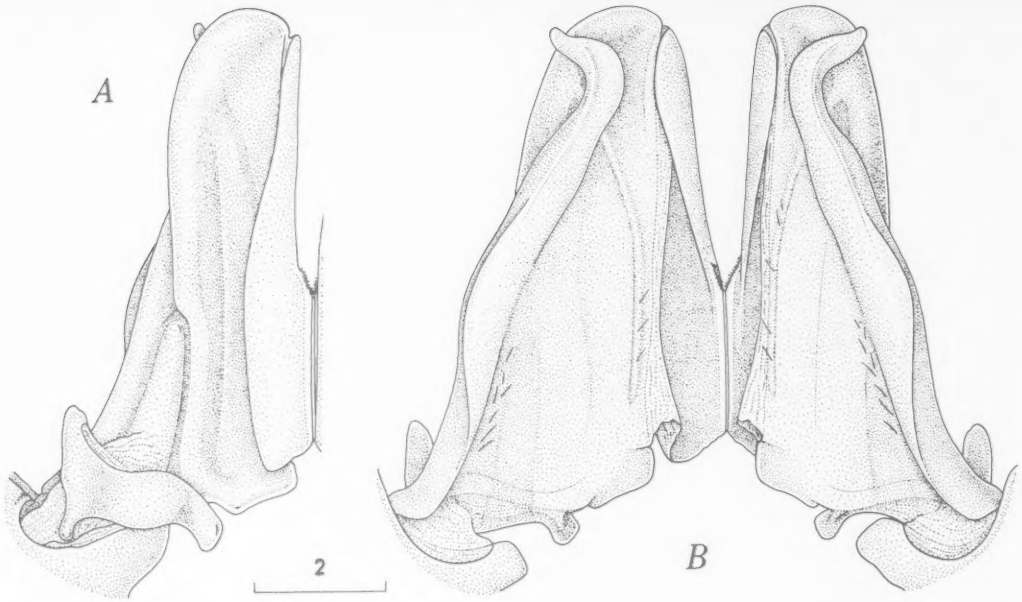

FIGURE 6.—*Hepomadus tener*. Petasma: A. Dorsal view of left half, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz. B. Ventral view of same petasma.

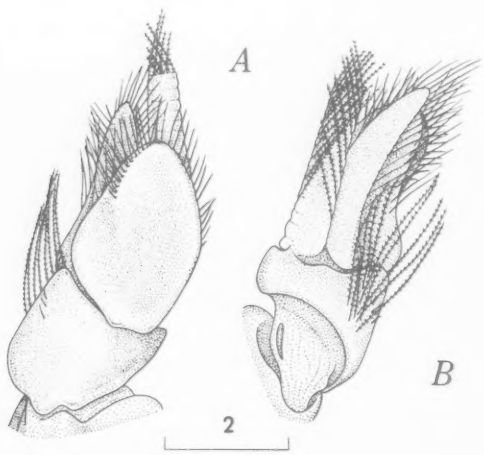

FIGURE 7.—*Hepomadus tener*. Appendices masculina and interna: A. Dorsal view of right appendix masculina and proximal part of endopod, ♂ 35.5 mm c.l., SE of Cabo Rojo, Veracruz. B. Ventral view, inclined slightly mesad, of appendices interna and masculina of same specimen.

Distribution

Off the Atlantic coast of the United States, from New Jersey southward, through the Sargasso Sea, to the Gulf of Mexico and Caribbean Sea, *H. tener* has been found at depths from 765 m (Roberts and Pequegnat, 1970) to about 5,400 m. This is the first time this species has been reported from the Caribbean, where it is widely distributed.

There are only two records of *H. tener* from localities outside the western Atlantic. Wood-Mason and Alcock (1891) questionably identified a much damaged female from the Bay of Bengal in 2,396 m. Later, Alcock (1901) apparently referring to the same specimen stated that the depth was 2305 m, and indicated that the epipod of the somite XIII consists of a tiny filament. This identification needs confirmation because the epipod is small, subrectangular and lamelliform in the western Atlantic material, as Burkenroad (1936) observed.

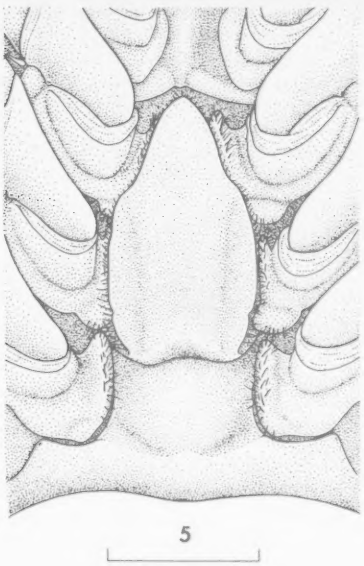

FIGURE 8.—*Hepomadus tener*. Thelycum, ♀ 47 mm c.l., off Back Bay, Va.

The other record is that of a female reported by Ramadan (1938) from off Zanzibar [Tanzania], in 2,930 m; this record leaves no doubt as to the presence of *H. tener* in the western Indian Ocean.

DISCUSSION

Previous authors (Smith, 1886; Bouvier, 1908; Burkenroad, 1936; Roberts and Pequegnat, 1970) who have reported *H. tener* from the western Atlantic have cited a number of differences between their material and specimens that had been described earlier. In addition to these western Atlantic records of this species, Milne Edwards and Bouvier (1909) identified a male from SW of Dry Tortugas Islands as *H. glacialis* on the basis of several features, including the presence of a well-defined spine on the midposterior margin of the fourth and fifth pleonic terga but, at the same time, pointed out other characters that distinguish their specimen from the type of *H. glacialis*.

Burkenroad (1936) presented a detailed discussion of the differences in various characters (e.g., shape of the proximal projection, "inner lobe," of the second segment of the mandibular palp, relative lengths of the stylocerite and the scaphocerite, development of the postrostral carina, length of the spine at the midposterior margin of the third pleonic tergum) among known specimens of *H. tener*, and interpreted the differences as individual variations or those due to differential growth rates. He also noted that the small male assigned to *H. glacialis* by Milne Edwards and Bouvier differs from *H. tener* (according to their description), in possessing a larger rostrum, a smaller interval between the last two rostral teeth, a shorter spine on the third pleonic tergum, an obtuse posteroventral tooth on each side of the sixth pleonic somite, and in lacking setae on the upper side of the endite of the basis of the second maxilla. He concluded that if such differences exist, the small male belongs to a species other than *H. tener*. Furthermore, Burkenroad stated that his specimens had no trace of a spine at the midposterior margin of the fourth and fifth pleonic terga, and that the presence of those spines in the male reported by Milne Edwards and Bouvier is the strongest reason for identifying the latter as *H. glacialis*. Later, Ramadan (1938) after examining the type of *H. glacialis*, cited three features by which Milne Edwards' and Bouvier's specimen differs from the type, and suggested that it probably represents an undescribed species.

The study of collections at my disposal as well as data presented in previous descriptions of other material indicate that all known western Atlantic *Hepomadus* are different from *H. glacialis*. During the course of the investigation it also has become evident that a considerable degree of variation exists among specimens from the region. In each of the characters considered, however, there is a broad range of variation, which seems to indicate that all the specimens belong to a single species, *Hepomadus tener*.

The principal differences between *H. glacialis*, the holotype of which has been made available to me, and *H. tener* are given in Table 1.

To analyze the various characters considered by previous authors to be of possible diagnostic

TABLE 1.—Characteristics distinguishing *Hepomadus glacialis* (holotype) from *H. tener*.

Feature	*H. glacialis* (holotype)	*H. tener*
Dorsum of carapace	Strongly arched to postcervical sulcus	Almost straight or very slightly arched, convexity extending beyond postcervical sulcus
Postrostral carina	Interrupted, disappearing on cardiac region, becoming distinct again and extending almost to posterior margin of carapace	Uninterrupted, extending posteriorly about 0.8 length of carapace
Setae on endite of basis of second maxilla		
Upper side	5 and 6 strong, 10 and 4 weak (right and left endite, respectively)	0; 2-4 strong, 1-4 weak
Lower side	5 and 9 strong, 3 and 5 weak	0; 2-5 strong, 1-4 weak

value in differentiating two species of western Atlantic *Hepomadus*, I have divided the material into three somewhat arbitrary groups based on the shape of the midposterior margin of the fourth and fifth pleonic terga: Group 1, straight; Group 2, slightly produced into a short, sometimes barely perceptible, projection; and Group 3, produced into a conspicuous spine. Intermediate stages (Group 2) between the two extremes (Groups 1 and 3) have not been discussed previously, although Bouvier (1908), in his description of a male *H. tener* from the Sargasso Sea, indicated that the dorsal carina of the fourth and fifth pleonic terga is produced into a small projection.

As stated above, Burkenroad indicated that in the specimen reported by Milne Edwards and Bouvier, which fits into Group 3, the interval between the last two rostral teeth is smaller than in the specimens with straight margins (Group 1) he had studied. I have found that this tooth interval varies considerably, from 0.30 to almost 0.60 of the distance between the first and the second tooth, and that the variations are not correlated with the shape of the posterior margin of the pleonic terga (Figure 9). It is true that according to the figure of Milne Edwards and Bouvier, in their Group 3 male (17 mm c.l.), the interval is 0.30, whereas in the Group 2 male described by Bouvier, the interval is 0.55 [according to his Figure 2, on plate 13], and in the female with 47 mm c.l., from off Virginia, belonging to Group 1, which Burkenroad had studied, the interval is 0.50. However, in the male holotype of *H. tener* (17.5 mm c.l., Group 1), which Burkenroad had not seen, the interval is 0.30, as in the 17 mm c.l. male of Group 3. Furthermore, among the material I have examined, two females of Group 3 of about same size (36 mm c.l. and 37 mm c.l.) possess a tooth interval of 0.40 and 0.60. Finally, in a small female of 14.5 mm c.l. and in another of 47 mm c.l., both belonging to Group 2, the tooth interval is about the same, 0.35 and 0.40, respectively. The data presented herein demonstrate that there are no significant differences in the tooth interval between the three groups.

The available information is too meager—particularly on animals of Group 1—to determine whether or not a clear correlation exists between the relative length of the rostrum and the shape of the midposterior margin of the fourth and fifth pleonic terga. Nevertheless, the ratio of the length of the rostrum to the length of the carapace in the specimens examined by me are presented in Table 2.

The relative length of the posteromedian spine on the third pleonic tergum varies greatly, from 0.3 of, to equivalent to, the distance between the transverse groove and the posterior margin of the tergum (adjacent to base of spine). The correlation of this ratio with increase in size of the animals seems obscure, and the correlation of the relative length of the spine with the shape of the midposterior margin of the fourth and fifth pleonic terga does not appear to indicate the presence of more than

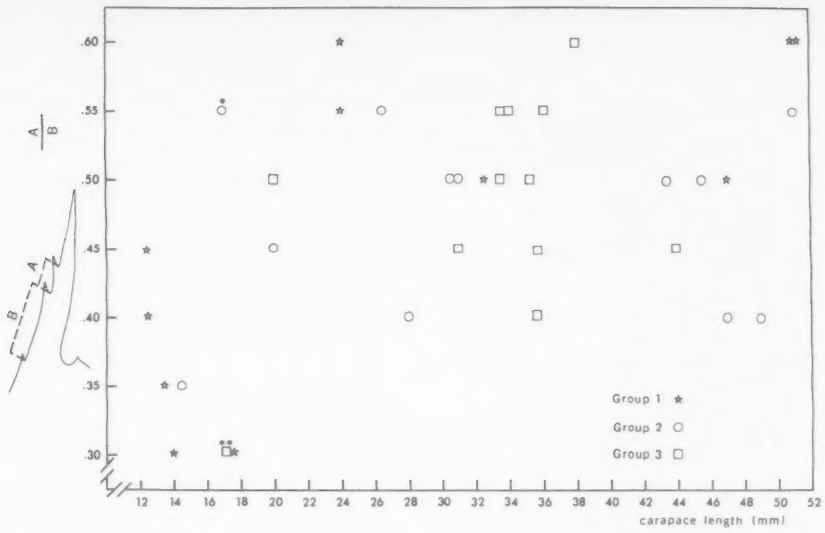

FIGURE 9.—Ratio of interval between last two rostral teeth (A) to interval between first two teeth (B) plotted against carapace length in the three groups (see text) of *Hepomadus tener*.

* Bouvier, 1908, pl. 13, fig. 2.
** A. Milne Edwards and Bouvier, 1909, pl. 1, fig. 3.

TABLE 2.—Ratio of rostrum length to carapace length at various carapace lengths (c.l.) in the three groups (see text) of *Hepomadus tener*.

c.l.	Group 1	Group 2	Group 3
12.5	♀ 0.45	—	—
	♀ 0.55	—	—
14	♂ 0.55	—	—
14.5	—	♀ 0.60	—
17.5	♂ 0.45	—	—
20	—	—	♂ 0.65
24	♂ 0.70	—	—
28	—	♂ 0.50	—
30.5	—	♀ 0.60	—
31	—	—	♂ 0.55
33.5	—	—	♀ 1.00
34	—	—	♂ 0.60
35.5	—	—	♂ 0.60
36	—	—	♀ 1.10
37	—	—	♀ 1.10
43.5	—	♀ 0.90	—
44	—	—	♀ 0.90
45.5	—	♂ 0.70	—
51	—	♀ 1.25	—

one species. In the specimens of Group 1, the ratio varies from 0.55 to 0.90 (Figure 10), in those of Group 2, from 0.30 to 1.0, and finally, in specimens of Group 3 the ratio varies from 0.30 to 0.45, except for a single individual in which the ratio is 0.55. It thus seems as if the specimens of Group 1 possess a longer spine on the third pleonic tergum than those of Group 3, but in specimens of Group 2 that spine may be as long as, or even longer, than in the specimens of Group 1, or as short as in those of Group 3.

The setation of the endite of the basis of the second maxilla varies within the same limits in the three groups, i.e., 0, or 2 to 4 strong and 1 to 4 weak setae on the upper side; and 0, or 2 to 5 strong and 1 to 4 weak setae on the lower side. Inasmuch as setae are found in many combinations and are lacking on the lower side in a few of the specimens examined by me, it seems highly probable that the absence of setae from the upper side of the endite in the specimen reported by Milne Edwards and Bouvier (1909) may very well fall within the range of individual variation within the species. I have not seen this specimen which is neither in the collection nor is it registered in the card catalog of the Museum of Comparative Zoology (Herbert W. Levi, pers. comm.).

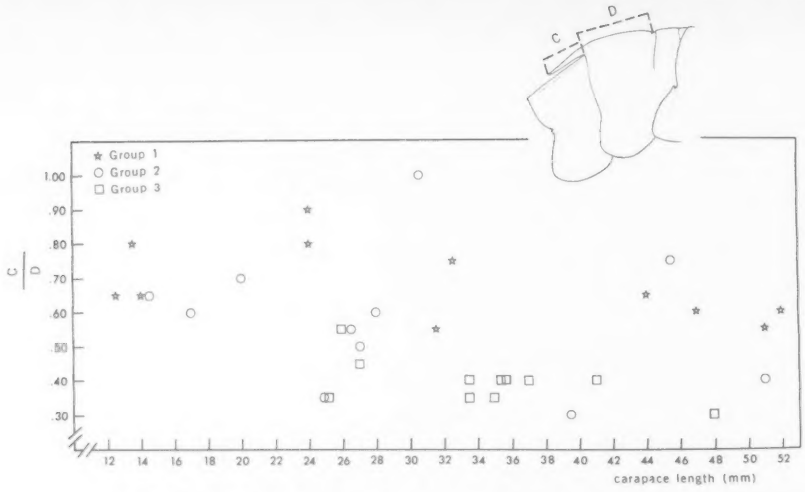

FIGURE 10.—Ratio of length of spine (C) on third pleonic tergum to distance between transverse groove and posterior margin of tergum (D) plotted against carapace length in the three groups (see text) of *Hepomadus tener*.

The differences which earlier authors have pointed out in the labrum, "epistome," among *Hepomadus*, seem to be due to changes in the relative position of its two lobes in preserved specimens. The posteroventral lobe may be only slightly raised and continuous with the anterodorsal lobe, or the posteroventral lobe may be thrust over the anterodorsal so that the two lobes become distinctly delimited.

Another character that has been cited as supposedly useful in differentiating species of *Hepomadus* in the western Atlantic is the shape of the posteroventral teeth of the sixth pleonic somite; however, it is variable, ranging from broadly triangular to subspiniform, in all three groups.

In addition to the features which have been studied by previous workers and discussed above, I have found that the length of the third pair of maxillipeds and five pairs of pereopods shows individual variation, but no consistent differences occur between the three groups; furthermore, the appendix interna may fall short or overreach the appendix masculina within each group, and also the two cicatrices on the sixth abdominal somite not only may be widely separated or almost fused within each group, but also both extremes are found in specimens of a single lot (e.g., 1 ♂ 1 ♀ taken off Alabama, at *Albatross* stn 2379).

The three groups of *H. tener* are not geographically isolated, but Groups 1 and 2 have been found off the east coast of the United States, the former ranging southward to the Bahamas and the latter to the Sargasso Sea. All three groups live in the Gulf of Mexico and the Caribbean Sea.

ACKNOWLEDGMENTS

I am indebted to Willard D. Hartman (YPM), Willis E. Pequegnat (TAMU), and Gilbert L. Voss (UMML) for making material available; also to Anthony L. Rice of the British Museum (Natural History) for placing at my disposal the holotype of *Hepomadus glacialis* Bate. Grateful acknowledgment is extended to Horton H. Hobbs, Jr., of the Smithsonian Institution (SI); Bruce B. Collette of the Systematics Laboratory, National Marine Fisheries Service, NOAA (NMFS), for invaluable suggestions made during the preparation of this work; and Thomas E. Bowman (SI) and

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LITERATURE CITED

ALCOCK, A.
1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine survey ship *Investigator*. Indian Museum, Calcutta v + 286 p., 3 pl.

BATE, C. S.
1881. On the Penaeidea. Ann. Mag. Nat. Hist., Ser. 5, 8:169-196, pl. 11-12.
1888. Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873-1876. Rep. Sci. Results Voyage H.M.S. *Challenger*. Zool. 24, xc + 942 p., 76 fig., 150 pl.

BOUVIER, E.-L.
1908. Crustacés décapodes (Pénéidés) provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice* (1886-1907). Résultats Campagnes Sci. Monaco 33, 122 p., 16 pl.

BURKENROAD, M. D.
1936. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. Materials for a revision of the oceanic Penaeidae. Bull. Bingham Oceanogr. Collect. Yale Univ. 5(2), 151 p., fig. 1-71.

MILNE EDWARDS, A., AND E. L. BOUVIER.
1909. Les pénéides et sténopides. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic Coast of the United States (1880), by the U.S. Coast Survey steamer *Blake*. XLIV. Mem. Mus. Comp. Zool., Harvard Univ. 27:179-274, 91 fig., 9 pl.

PEQUEGNAT, W. E., AND T. W. ROBERTS.
1971. Decapod shrimps of the family Penaeidae. *In* W. E. Pequegnat, R. W. Firth, Jr., B. M. James, and T. W. Roberts, Gulf of Mexico deep-sea fauna Decapoda and Euphasiacea, p. 8-9. Ser. Atlas Mar. Environ. Am. Geogr. Soc. Folio 20.

RAMADAN, M. M.
1938. Crustacea: Penaeidae. John Murray Exped. 1933-34, Sci. Rep. 5:35-76, fig. 1-15.

ROBERTS, T. W., AND W. E. PEQUEGNAT.
1970. Deep-water decapod shrimps of the family Penaeidae. *In* W. E. Pequegnat and F. A. Chace, Jr. (editors), Contributions on the biology of the Gulf of Mexico, p. 21-57, fig. 3-1, 3-2, 3-3A, 3-3B, 3-4. Tex. A&M Univ. Oceanogr. Stud. 1.

SMITH, S. I.
1884. Report on the decapod Crustacea of the *Albatross* dredgings off the east coast of the United States in 1883. Rep. U.S. Comm. Fish Fish. 10:345-426, pl. 1-10.
1887. Report on the decapod Crustacea of the *Albatross* dredgings off the east coast of the United States during the summer and autumn of 1884. Rep. U.S. Comm. Fish Fish. 13:605-705, pl. 1-20.

WOOD-MASON, J., AND A. ALCOCK.
1891. Natural History notes from H.M. Indian Marine Survey steamer 'Investigator,' Commander R. F. Hoskyn, R.N., commanding. No. 21. Note on the results of the last season's deep-sea dredging. Ann. Mag. Nat. Hist., Ser. 6, 7:1-19, 186-202, 258-272, fig. 1-5.

HELMINTH PARASITES OF PORPOISES OF THE GENUS *STENELLA* IN THE EASTERN TROPICAL PACIFIC, WITH DESCRIPTIONS OF TWO NEW SPECIES: *MASTIGONEMA STENELLAE* GEN. ET SP. N. (NEMATODA: SPIRUROIDEA) AND *ZALOPHOTREMA PACIFICUM* SP. N. (TREMATODA: DIGENEA)

MURRAY D. DAILEY[1] AND WILLIAM F. PERRIN[2]

ABSTRACT

Parasite frequencies in 72 spotted porpoise, *Stenella graffmani* (Lönnberg, 1934), and 19 spinner porpoise, *S.* cf. *S. longirostris* (Gray, 1828), are reported and analyzed with respect to age of host. In addition to the new nematode *Mastigonema stenellae* gen. et sp. n. from the fore stomach of *S. graffmani* and the new fluke *Zalophotrema pacificum* sp. n. from the pancreatic duct of *S. graffmani* and *S.* cf. *S. longirostris*, parasites reported include *Anisakis simplex*, *Halocercus delphini*, *Crassicauda* sp., *Campula rochebruni*, *Tetrabothrium forsteri*, *Strobilocephalus triangularis*, *Phyllobothrium delphini*, and *Monorygma grimaldii*. Irreversible lesions in the ventral region of the skull due to infection of the air sinuses by a *Crassicauda*-like nematode were more frequent in skulls of calves of *S. graffmani* than in skulls of subadults and adults (129 specimens total), indicating that the parasite, or a condition correlated with its occurrence, is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

Porpoises of the genus *Stenella* are of great importance to the U.S. tropical tuna fishery (Perrin, 1969, 1970a). Yellowfin tuna associate with porpoise schools in the eastern Pacific, and the fishermen make use of this association in locating and capturing the tuna. Despite this economic importance, little is known of the ecology of the porpoises. Parasites have been previously reported from *Stenella longirostris*, *S. roseiventris*, *S. coeruleoalba*, *S. attenuata*, and *S. graffmani* (Dailey and Brownell, 1972). These reports have usually been from a small sample and did not include numbers of parasites per animal or percentage of sample infected. This report deals with two members of the genus in the eastern tropical Pacific: the spotted porpoise and the spinner porpoise. The taxonomy of the genus is currently in a chaotic state. Spinner porpoises from the eastern Pacific have been referred by recent authors to *Stenella microps* (Gray, 1846) and to *S. longirostris* (Gray, 1828)—Perrin and Hunter (1972). The spotted porpoise *S. graffmani* (Lönnberg, 1934) was described from Acapulco, but Rice and Scheffer (1968) recently referred all spotted porpoises to *S. dubia* (G. Cuvier, 1812), a decision that does not reflect a concensus of current opinion (Perrin, 1970b; Mitchell, 1970; Caldwell et al., 1971). We here refer the spotted porpoise examined to *S. graffmani* and the spinner porpoise tentatively to *S. longirostris*. The "eastern" and "whitebelly" spinner porpoises (Perrin, 1972) are considered to be geographical variants within one species and are not treated separately. This usage is provisional pending the results of current taxonomic investigations.

MATERIALS AND METHODS

We examined 72 specimens of *S. graffmani* and 19 of *S.* cf. *S. longirostris* (11 eastern and 8 whitebelly). These were collected during the course of investigations of morphology and reproduction. We collected parasites as we prepared skeletons of the animals for use

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as museum specimens. Capture data and museum numbers are presented in Appendix Tables 1 and 2. Also, we examined 67 skulls of spotted porpoise and 29 of spinner porpoise from museum collections, for bone damage caused by nematode infection. The museum specimens were from the eastern tropical Pacific and are listed below. Abbreviations used are: AMNH, American Museum of Natural History, New York; LACM, Los Angeles County Museum; SDMNH, San Diego Museum of Natural History; USNM, United States National Museum, Washington, D.C.

S. graffmani: AMNH130216, LACM27412, 27413, 27419, 27420, 27421, 27422, 27425, 27426, 27427, 27428, 27429, 27431, 27434, 31362, 31431; SDMNH20637, 21199; USNM-261427, 261428, 261429, 261430, 261431, 261432, 261433, 261434, 395264, 395265, 395266, 395267, 395268, 395615, 395616, 395617, 395618, 395926, 395927, 395928, 395929, 395935, 395936, 395937, 395938, 396027, 396029, 396034, 396037. The following LACM specimens, identified by field numbers, had no museum numbers when examined: GDF42, GDF57, MI563, RLB404, RLB500, WAW42, WAW51, WAW55. The following specimens, identified by field numbers are in the research collection at the Southwest Fisheries Center (SWFC below), La Jolla, Calif: CV160, JSL88, JSL89, JSL90, JSL95, RICE65-1, RICE66-3, WFP7, WPSG-01, WPSG02, WPSG03.

S. cf. *S. longirostris:* LACM27414, 27423, 27424, 27428, 27430, 27432, 27433; SDMNH-21200, 21427; USNM395269, 395270, 395271, 395272, 395273, 395274, 395275, 395930, 395931, 395932, 395933, 395934, 396030, 396032, 396035; LACM field numbers GDF56, RLB238, RLB405, WAW43, WAW50, WAW-52, WAW53, WAW54, WAW58, WAW60; SWFC field numbers CV240, CV241, CV245, RICE65-149, RICE67-102.

While rough-cleaning the porpoise carcasses for skeletal preparation, we examined the blubber, mesenteries, peritoneum, musculature, blowhole region, maxillary sinuses, mammary glands, and viscera (esophagus, stomachs, heart, lungs, liver, spleen, kidneys, gonads, intestine) for larval and adult parasites. We searched 3-m lengths of the intestine at the duodenal end, mid-length, and posterior end. Counts of cysts in the blubber should be considered as relative indices; we did not examine all the blubber carefully. We filled out a data form for each carcass indicating precisely which areas had been checked for parasites. All worms and cysts were fixed in Lavdowsky's (Formalin[3]-Acetic acid-Alcohol) or Bouin's fluid and stored in 70% ethanol. Cestode, trematode, and acanthocephalan whole mounts were stained with celestine blue B or Semichon's carmine. Specimens were sectioned singly or in situ at 6, 8, and 10 μ and stained with Mayer's hematoxylin and eosin Y or Mallory's trichrome. All material except nematode whole mounts were dehydrated in ethanol, cleared in xylene, and mounted in Piccolyte. Nematodes were cleared and mounted in glycerine. Drawings were made with the aid of a drawing tube. Measurements are given in millimeters unless otherwise stated. Average measurements are given with ranges in parentheses.

THE PARASITES

Counts of parasites collected are tabulated in Appendix Tables 1 and 2.

Nematoda

Anisakis simplex (Rudolphi, 1809, det. Krabbe, 1878)

This nematode was the most frequent parasite collected during this study. The taxonomic criteria used in identification of these specimens were those presented by Davey (1971) in his revision of the genus *Anisakis*. *A. simplex* was found in the stomachs of both host species and represents a new host report for both *S. graffmani* and *S. longirostris*. Anisakids have been previously reported from other species of *Stenella* (Delyamure, 1955; Kagei et al., 1967; Zam, Caldwell, and Caldwell, 1971; Dailey and Brownell, 1972).

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Halocercus delphini Baylis and Daubney, 1925

This parasite has been reported previously from the genus *Stenella* by Zam et al. (1971). They found three of 17 *S. plagiodon* (Cope, 1866) taken off the Florida coast infected with *H. delphini*. This report represents a new host record from *S. graffmani* and *S. longirostris*. Infections occurred in bunches with the anterior ends of the parasites embedded in capsules found outside of the bronchial walls (Figure 1). The body of each parasite lies in the bronchiole oriented in an anterior direction, never towards the apex of the lobe, similar to the orientation described for *Skrjabinalius cryptocephalus* (see Delyamure, 1955).

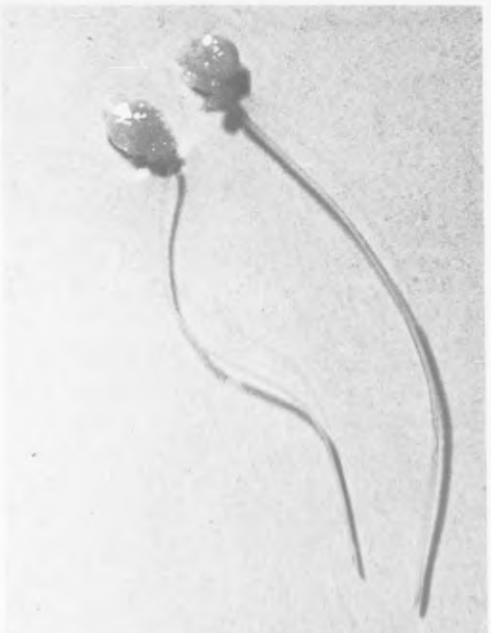


FIGURE 1.—*Halocercus delphini* with anterior end embedded in capsule. (X7)

Mastigonema stenellae gen. et sp. n. (Nematoda: Spiruridae)

This nematode is described from three female specimens taken from the forestomachs of two *S. graffmani* (both recovered prior to present study) and one *S. longirostris*.

Mastigonema gen. n. (Ascaropsinae)

Mouth with two unlobed lips. Cervical cuticle not inflated or flanged. Buccal capsule cylindrical, with few connecting, annular, thickenings. Esophagus long, not divided into anterior and posterior portions; valve of typical spiruroid form. Females prodelphic, ovaries postesophageal. Vulva in middle third of body. Cuticle transversely striated. Oviparous. Parasites of Cetacea.

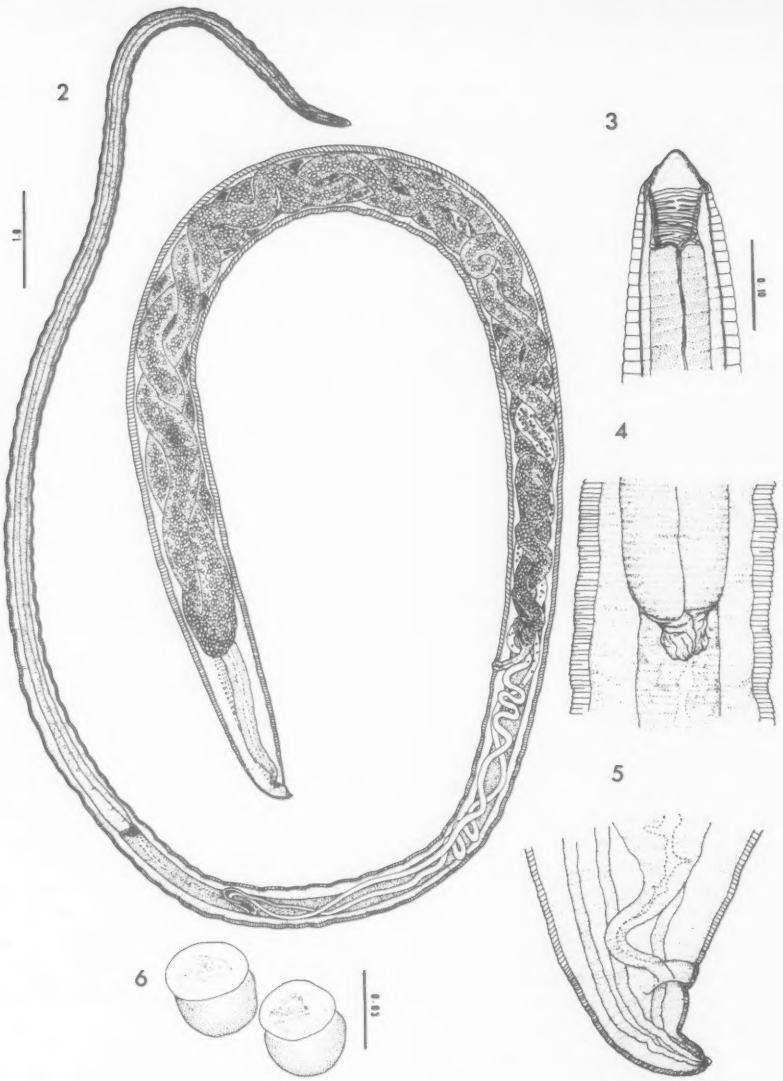
Mastigonema stenellae sp. n. (Figures 2-6)

With characters of the genus: body whip-shaped, with thin anterior and enlarged posterior portions. Stoma triangular; two large lips. Buccal capsule reinforced with connecting rings, cervical papillae present, eggs with enlarged cap.

Female: 25.5 (23.5-28.5) long by 1.2 in maximum width, 7.0 from posterior end. Buccal capsule 0.054 long, tapering from 0.045 wide at anterior to 0.032 at esophageal junction. Nerve ring 0.281 from anterior end, surrounding esophagus. Esophagus 8.5-11.7 long, widening at approximately 2.59 from anterior end. Ovaries directed anteriorly then reflexing sharply. Vulva muscular, 16.64 from anterior, vagina vera 0.13 long by 0.086 wide, vagina uterina 0.81 long by 0.11 wide. Eggs 0.034 long by 0.032 wide, with swollen cap slightly larger than bottom portion. Anal lip large, anus 0.22 from posterior tip. Tail conical with large mucron.

Hosts: *Stenella graffmani*, *S. longirostris*.
Location: Forestomach.
Locality: Eastern tropical Pacific Ocean; holotype from *S. longirostris* collected at approximately lat 8°N, long 107°W.
Type specimens: USNM Helminth Collection holotype female No. 72159, paratype No. 72160.

Remarks: A search of the literature indicates this is the first report of a spirurid



FIGURES 2-6.—*Mastigonema stenellae* sp. n.: 2. Entire worm. 3. Cephalic region, showing annular thickenings. 4. Esophageal-intestinal valve. 5. Caudal region. 6. Eggs, showing enlarged caps.

nematode parasitizing a marine mammal. The general body shape of this nematode is similar to that seen in *Vasorhabdochona cablei* Martin and Zam, 1967, *Trichospirura leptostoma* Smith and Chitwood, 1967, and *Freitasia teixeirai* Baruš and Coy, 1965. However, the structure of lips and buccal capsule place it in the subfamily Ascaropsinae rather than with the rhabdochonids. Of the genera in this subfamily it most closely resembles the genus *Pereirai* Cuocolo, 1943. It differs from *Pereirai* in the following characteristics; lips are unlobed, cuticular flange is lacking, buccal capsule has few annular thickenings, esophagus not divided into anterior and posterior portions, and vulva in posterior half of body.

Crassicaudidae Skrjabin et Andrews, 1934

Crassicauda sp. A single infection of this tissue nematode was found in the 78 animals examined (1.3%). The worms were in the abdominal muscle adjacent to the mammary gland of *S. longirostris*. A large abdominal cyst was also found in the same area. Sections revealed large numbers of *Crassicauda* sp. eggs as well as portions of the female worm (Figure 7). Entire worms were not recovered so specific identification was not possible. However, egg

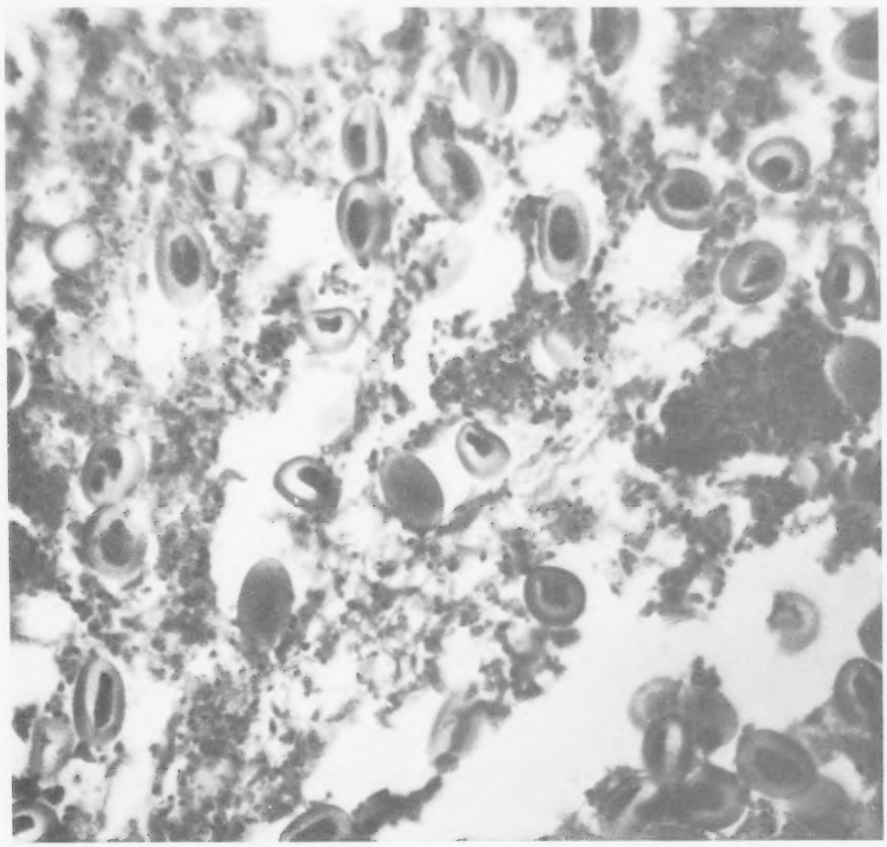


FIGURE 7.—Section through abdominal cyst with *Crassicauda* eggs. (X150)

measurements resemble those given for *C. grampicola* by Johnston and Mawson (1941) from Risso's porpoise, *Grampus griseus* (Cuvier, 1812), taken at New South Wales, Australia.

Another single specimen with *Crassicauda* affinities was recovered by James G. Mead, University of Chicago, Department of Anatomy, while dissecting the head of a *S. graffmani*. The worm was taken from the pterygoid air sinus. The pterygoid bone was eroded in the region in which the specimen was found. We assume that extensive bone damage found by us in other specimens we examined (Figure 8) was also caused by infestations of this nematode, although, judging from the published literature, the possibility cannot be dismissed that more than one species is involved. Reysenbach de Haan (1957) reported *Stenurus globicephalae* Baylis and Daubney, 1952, in the sinuses and cava tympani of the pilot whale, *Globicephala melaena* (Traill, 1809). Norris and Prescott (1961) collected "large quantities of a nematode (*Stenurus* sp.)" from the lateral air sinus of a dall porpoise, *Phocoenoides dalli* (True, 1885). Tomilin and Smyshlyayev (1968) reported that a "nematode *Stenurus minor* attacks the hearing organs of the Black Sea porpoise *Phocaena* and by clogging the cavity around the earbone may kill its host or severely complicate its existence." Brodie (1971) reported *Crassicauda* sp. as a middle ear parasite of the white whale, *Delphinapterus leucas* Pallas, 1776, in Cumberland Sound, Baffin Island. Yamada (1956) examined skulls of approximately 80 false killer whales, *Pseudorca crassidens*, from a stranded group of approximately 150 and found "basket-like" lesions in the pterygoid region of 40 skulls. He ascribed the damage to parasitic infection, "most probably by nematodes," and stated that such damage is a common occurrence in *Grampus* and *Globicephala* in Japanese waters.

Trematoda

The trematodes recovered during this study are represented by two genera known from marine mammals and three specimens of one genus that has been found in teleost hosts.

Zalophotrema pacificum sp. n.
(Figures 9 and 10)

Description: Based on measurements from 26 specimens. With characteristics of the genus. Body elongate. Dorsoventrally flattened, 10 mm (8.3-12.6) long by 1.7 mm (1.4-2.0) wide. Cuticle spinose. Oral sucker 535 μ (398-592) long by 575 μ (439-673) wide; opening slightly subterminal. Pharynx pyriform, 494 μ (398-541) long by 314 μ (255-367) wide. Intestinal cecum bifurcates immediately caudad to pharynx with each lateral branch dividing into short anterior and long posterior portions. Both anterior and posterior cecal branches contain numerous diverticula; anterior branch terminating lateral to posterior edge of oral sucker, posterior branch terminating near posterior end of body. Excretory pore terminal. Acetabulum 600 μ (520-710) in diameter, located approximately mid-body. Cirrus unarmed. Testes large, lobed, in tandem and extending posterior to equatorial third of body. Ovary pretesticular, lobed, 333 μ (235-418) long by 477 μ (310-765) wide. Mehlis's gland posterior and dorsal to ovary. Uterus coiled, preovarian. Genital pore just preacetabular. Vitellaria follicular, occupying entire anterior half of body from level of genital pore to shoulder region of ceca, extending posterior from genital pore in lateral bands to posterior end of body. Eggs, oblong, operculate, round in cross-section, mean measurements of 20 eggs, 61 μ long by 42 μ wide.

Hosts: *Stenella longirostris, Stenella graffmani.*

Location: Pancreatic duct.

Locality: Eastern tropical Pacific Ocean; holotype from *S. graffmani* collected at lat 12°5'N, long 93°18'W.

Type specimen: USNM Helm. Coll. No. 72158.

Remarks: Currently there are three species in the genus *Zalophotrema* (Stunkard and Alvey, 1929): *Z. hepaticum* Stunkard and Alvey, 1929, described from the bile ducts of a California sea lion, *Zalophus californianus* (Lesson, 1828), at the New York Aquarium; *Z. curilensis* Gubanov, 1952, from the bile ducts of

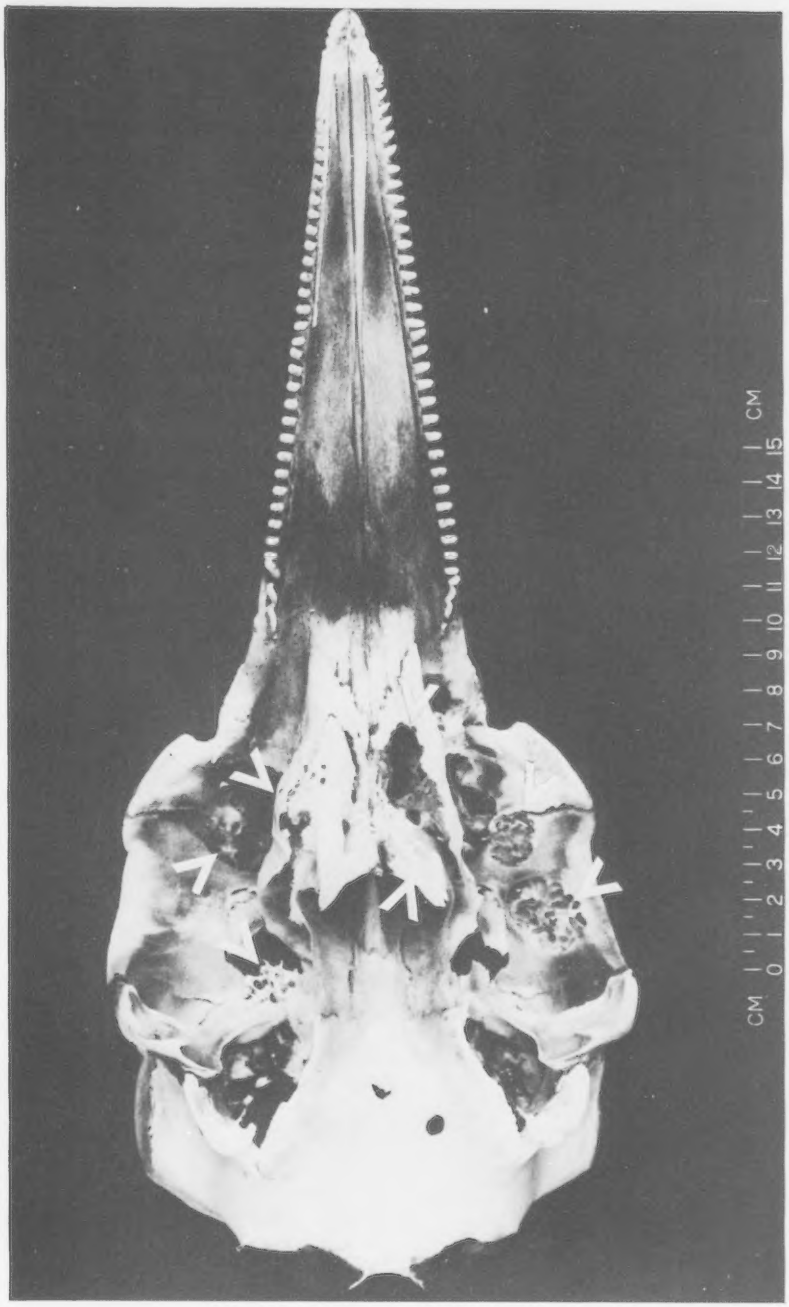
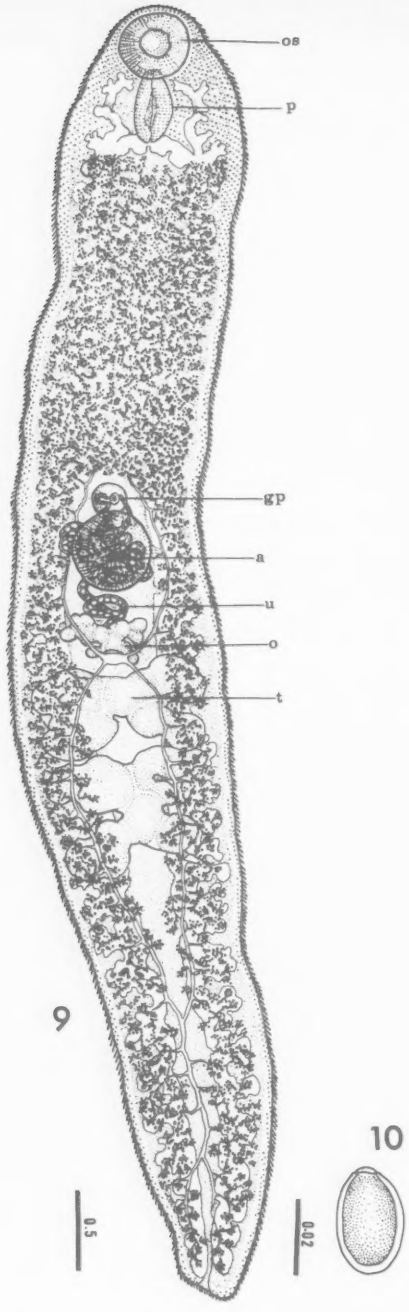


FIGURE 8.—Ventral view of skull of spotted porpoise, *Stenella graffmani*, showing bone lesions (arrows).



a sperm whale, *Physeter catodon* L; and *Z. lubimowi* Petrov and Chertkova, 1963, from the liver of a southern sea lion, *Otaria byronia* (Blainville, 1820) at the Moscow Zoo. *Zalophotrema pacificum* sp. n. can be easily separated from the three previously described species. *Z. lubimowi* differs from all other species in the genus in that it does not have confluent vitellarian fields anteriorly. *Z. curilensis* differs from *Z. pacificum* by larger body size (18-22.5 mm long by 5-7 mm wide) as well as the acetabulum being larger than the oral sucker. *Z. pacificum* sp. n. is most similar to *Z. hepaticum* in general body shape but differs in the following characteristics: body width (*Z. hepaticum* 3.0-3.6 mm wide), sucker ratio (in *Z. hepaticum* oral sucker almost twice as large as acetabulum while in *Z. pacificum* sp. n. suckers are approximately same size), ratio of distance between suckers to body length (*Z. hepaticum* 1:13, *Z. pacificum* sp. n. 1:2.5), distribution (percentage) of preacetabular vitellaria (*Z. hepaticum* nearly twice as large as those of Z. pacificum sp. n.), and egg size (75 μ long by 50 μ wide in *Z. hepaticum*).

Campula rochebruni (Poirier, 1886)
Bittner et Sprehn, 1928

This parasite was recovered from the stomachs and hepatopancreatic ducts of three (two *S. graffmani* and one *S. longirostris*) of 78 (3.9%) animals examined. This is a new host record for this parasite and represents the first report from the genus *Stenella*. *C. rochebruni* was originally described from *Delphinus delphis* L. in European waters.

Incidental Trematodes

Three specimens of the genus *Hirudinella*

FIGURES 9-10.—*Zalophotrema pacificum* sp. n. 9. Entire worm, ventral view; 10. egg. Abbreviations used: a - acetabulum; gp - genital pore; o - ovary; os - oral sucker; p - pharynx; t - testis; u - uterus.

Garsin, 1730, were recovered from the forestomachs of three hosts (two *S. longirostris* and one *S. graffmani*). Members of this genus are commonly parasites of teleost fishes and were probably ingested with a meal of fish and not established parasites of these hosts.

Cestoda

Tetrabothrium forsteri (Krefft, 1871) Fuhrmann, 1904

This cestode was recovered from the intestine of over 50% of the examined hosts and occurred in both *S. graffmani* and *S. longirostris*. This is the first report of this parasite from either of these hosts. *T. forsteri* (Krefft, 1871) was first described by Krefft (1871) under the name of *Taenia forsteri* from *Delphinus delphis* L. (= *D. forsteri*) caught off the coast of New Zealand and later transferred to the genus *Tetrabothrium* by Fuhrmann (1904). A complete review of the literature on this species is given by Delyamure (1955).

Strobilocephalus triangularis (Diesing, 1850) Baer, 1932

This tetrabothriid has a complex taxonomic history that is covered by Delyamure (1955). The parasite apparently anchors its scolex in the colon wall when small and grows inside a fibrotic capsule formed by the host (Figures 11 and 12). This is the first report of this parasite from the genus *Stenella*. It has been reported from the Pacific Ocean by Baer (1955), who described material taken from an unidentified dolphin captured in the waters of the Marshall Islands. There are numerous reports of the parasite from Atlantic Ocean hosts (*Hyperoodon ampullatus*) (Forster, 1770) (= *H. rostratus*), *Mesoplodon bidens* (Sowerby, 1804), *Lagenorhynchus acutus* (Gray, 1828), *Steno bredanensis* Lesson, 1828 (= *S. frontatus*), *Delphinus* sp. (Delyamure, 1955).

Phyllobothrium delphini (Bosc, 1802) and *Monorygma grimaldii* (Moniez, 1881) Baylis, 1919

These larval cestodes were recovered from

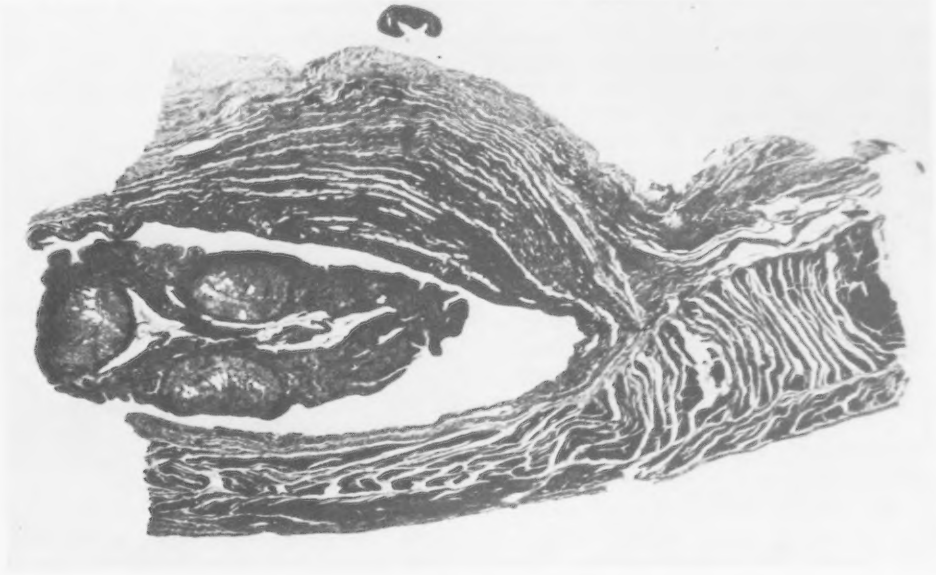


FIGURE 11.—Section through the capsule and scolex of *Strobilocephalus triangularis* from the rectum of *S. graffmani*. (X10.5)

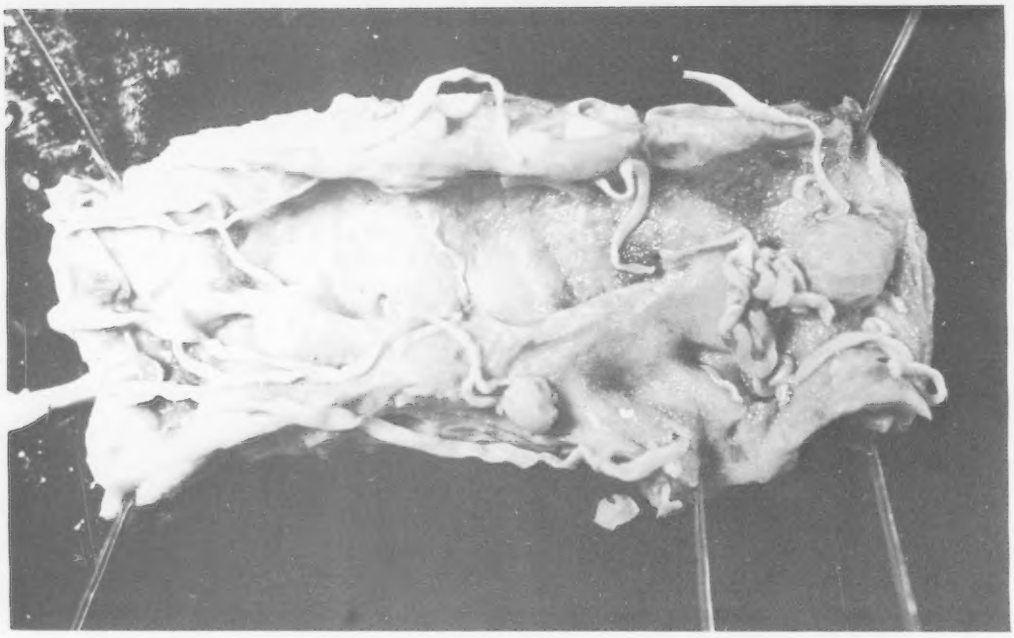


FIGURE 12.—*Strobilocephalus triangularis* attached in rectum of *Stenella graffmani*. (X1)

a large proportion of the animals examined. The history of these worms has been discussed by Delyamure (1955), Dollfus (1964), Williams (1968), and Dailey and Brownell (1972). *P. delphini* was always found in the blubber and *M. grimaldii* in the mesenteries.

PARASITE LOAD RELATIVE TO AGE OF HOST

The availability of data for a large sample of porpoise specimens, especially of *S. graffmani*, dissected in relatively uniform manner provides an unique opportunity to examine infection relative to age of the host for certain of the more frequently encountered parasite species. We discuss only the parasite species for which patterns of infestation are apparent in the data.

Spotted Porpoise, *Stenella graffmani*

The sample of *S. graffmani* examined may be divided into four age classes on the basis of total length, the developmental pattern categories defined by Perrin (1970b) and degree of sexual maturity (Figure 13). Females were classified as adult by the presence of corpora of ovulation in the ovaries and males by presence of spermatogenesis in the seminiferous tubules, as determined by histological examination. Sixty-one of the 72 specimens were collected during a 1-month period, and the first three modes probably represent discrete reproductive cohorts. Analysis below of parasitism relative to age is in terms of the four age classes, except as noted in the case of the *Crassicauda*-like nematode in the air sinuses.

The percent infection for *Anisakis* in *S. graffmani* shows increase with age of the host (Figure 14), but very large numbers of worms were found only in subadults, and the parasite number frequency distribution for that class is obviously skewed to the right. The inference to be drawn is that either some reduction in number of worms occurs in a heavily infected porpoise as it matures, due to the life cycle

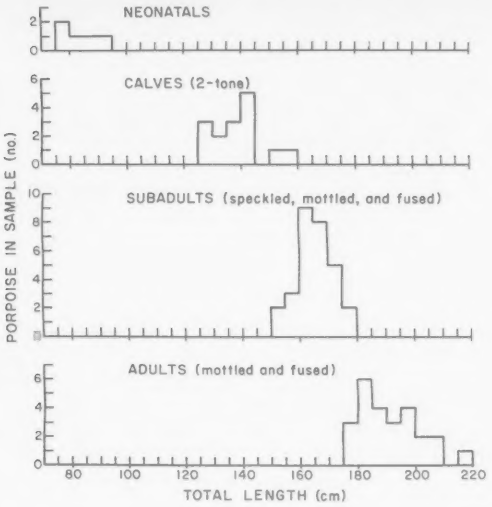


FIGURE 13.—Frequency distributions of total length, by age class, of spotted porpoise, *Stenella graffmani*, included in sample examined for parasites.

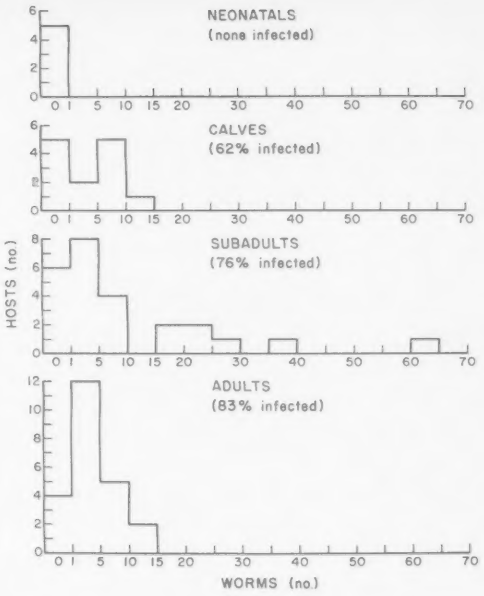


FIGURE 14.—Frequency distributions of levels of infection by *Anisakis* in four age classes of *Stenella graffmani*.

of the parasite and/or to possibly differential feeding habits of young and mature porpoise, or heavily infected individuals die before attaining maturity.

The case of the *Crassicauda*-like parasite in the air sinuses of *S. graffmani* certainly provides the most dramatic instance of infection varying with age. As stated above, the sinuses were not searched during dissection of most of the porpoise specimens, and only one specimen of the *Crassicauda*-type was recovered. Direct evidence, however, is provided of heavy infection by the areas of bone erosion on the lower surfaces of the skull (as illustrated in Figure 8). Given this circumstance, we expanded the series of porpoise specimens examined to include skeletal specimens in various museum collections. In all, 129 skulls of spotted porpoise from the eastern tropical Pacific were examined (see Materials and Methods). Since correlated data on size, reproductive condition, and color pattern were not available for most of the museum specimens examined, it was necessary to use other criteria of age for those specimens. The fetal and neonatal skulls examined were all from specimens we dissected. Those of the remaining skulls that were museum specimens were relegated to the three categories of calves, subadults, and adults by criteria of cranial features, using the sample of skulls from specimens we dissected to correlate these features with total length, sexual maturity, and color pattern. Museum skulls were assigned to the calf class when in condylobasal length, telescoping of facial elements, and closure of occipital sutures, they had not reached the adult condition. Skulls exhibiting adult length, telescoping, and occipital closure were divided into adults and subadults by the criterion of presence or absence of distal fusion of the premaxillary and maxillary bones of the rostrum. Rough correlation of the onset of fusion with attainment of sexual maturity was found among the skulls from specimens for which external data were also available (Table 1. Errors in classifying subadult skulls as adult and vice versa are approximately equal. Results of examination of the 129 skulls for bone damage (Table 2) demonstrate clearly that the rate of infection is very much higher in

TABLE 1.—Incidence of distal fusion of pmx (premaxillary) and mx (maxillary) bones in specimens of *Stenella graffmani*.

Age class[1]	Examined	Pmx and mx fused	Error in classification
Subadults	31	6	19.4%
Adult	21	18	14.3%

[1] As determined by criterion of total length, color pattern, and sexual maturity.

TABLE 2.—Lesions of the ventral side of the skull in *Stenella graffmani*, presumably due to infection by a *Crassicauda*-like nematode.

Age class	Range of condylobasal length	Examined	Lesions present
	(mm)		
Nearterm fetuses and neonatals	209-236	10	0
Calves	302-359	18	8 (44.4%)
Subadults	356-446	45	5 (11.1%)
Adults	360-466	56	4 (7.1%)
Total		129	17 (13.2%)

calves than in subadults or adults. What is more, the most severely damaged skulls were those of calves. Such extensive damage is certainly irreversible, in that if repaired, traces would still be apparent in the form of bone callouses, depressions, or altered shape of bone elements. No such traces were found in any of the adult skulls examined, although we searched for them carefully. We conclude, therefore, that heavy damage is indicative of a probably morbid condition and that parasitism or a correlated condition is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

The patterns of infection relative to age by cysts of the cestodes *Monorygma* and *Phyllobothrium* (Figure 15) closely resemble each other, with little or no occurrence before subadulthood and 100% occurrence and greatest numbers in adults. As these are larval forms, the cysts presumably would have to be ingested by predators of the porpoise in order for the life cycles of the parasites to progress. Killer whales, *Orcinus orca*, have been observed by Perrin to prey on spotted porpoise, and sharks of several species have been observed to feed on dead and injured spotted porpoise during tuna fishing operations (Leatherwood, Perrin, Garvie, and La Grange, manuscript).[4] Killer whales and/or sharks are therefore possible candidates for terminal hosts of these two cestodes, although adult Tetraphyllidea have only been found in elasmobranchs. However, a life cycle involving a warm blooded intermediate host serving a cold blooded definitive host has not been previously demonstrated.

The two nonlarval cestodes, *Tetrabothrium forsteri* (Figure 16) and *Strobilocephalus triangularis* (Table 3), exhibit different patterns of occurrence, more like those of the nematodes, occurring with greatest numbers and frequencies in calves in the case of *T. forsteri* and in calves and subadults in the case of *S. triangularis*. This was especially striking for *S. triangularis*. In the two calves and two subadults with extremely heavy infections, the last meter of the intestine was all but blocked and swollen to three or four times its normal diameter. No adult examined was found to be infected with *S. triangularis*.

Spinner Porpoise, *Stenella* cf. *S. longirostris*

The smaller sample of spinner porpoise was divided into three age classes on the basis of length and sexual maturity, with subadults again defined as immature animals of adult size. Despite the small number of data for the spinner (Appendix Table 2), some differences are apparent between the patterns of infection for this species and for *S. graffmani*. For *Anisakis*, the specimen with the greatest number of worms (CV285) was a large adult female, which contrasts with the finding for *S. graffmani*, in which heaviest infections occurred in subadults. Bone erosion suggesting severe infection of the ventral air sinuses by a nematode was encountered in only 1 skull (of a subadult) of 53 examined. The parasite specimen was not recovered, precluding identification, but the damage was similar to that caused by the *Crassicauda*-like nematode in *S. graffmani*.

[4] Leatherwood, J. S., W. F. Perrin, R. L. Garvie, and J. C. La Grange. Observations of sharks attacking porpoise (*Stenella* spp.). (Unpubl. manuscr.)

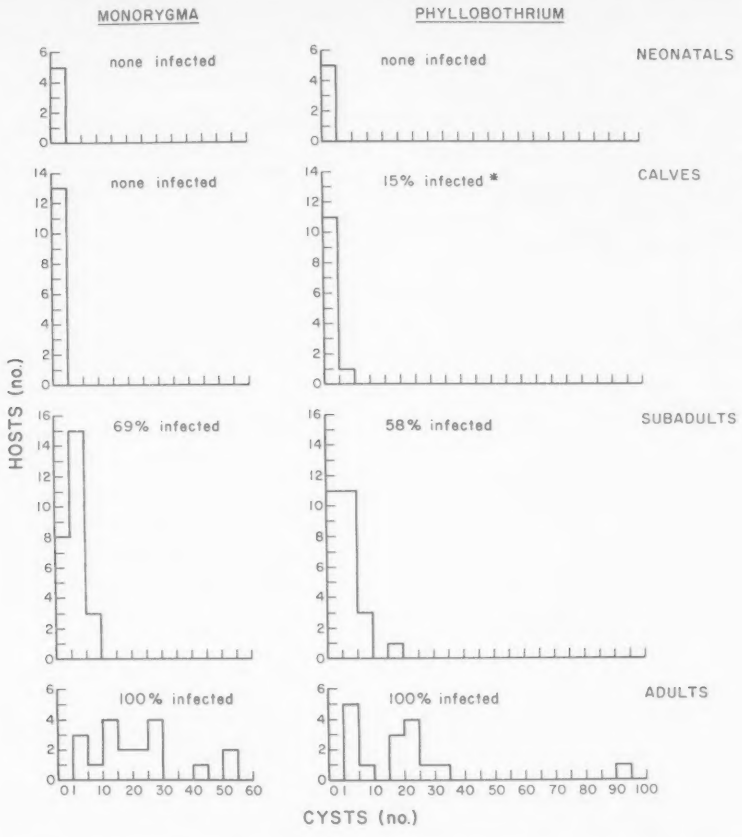


FIGURE 15.—Frequency distributions of levels of infection by cysts of *Monorygma grimaldii* and *Phyllobothrium delphini* in four age classes of *Stenella graffmani*.

Infection by cestode cysts showed the same pattern as in *S. graffmani*, except that one adult specimen was found to be free of *Phyllobothrium* cysts. Also, as in *S. graffmani*, calves were most heavily infected with *T. forsteri*, and *Strobilocephalus triangularis* was encountered only in an immature specimen, a calf.

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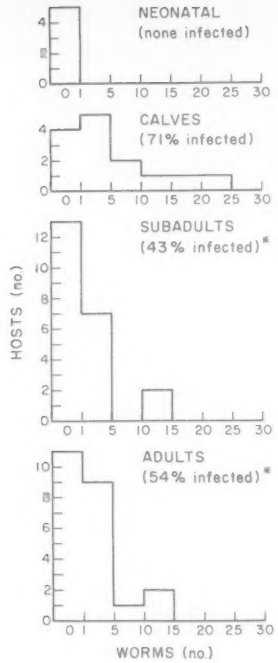

FIGURE 16.—Frequency distributions of levels of infection by *Tetrabothrium forsteri* in four age classes of *Stenella graffmani*.

TABLE 3.—*Strobilocephalus triangularis* in *Stenella graffmani*.

Age class	Examined	Infected
Neontals	5	0
Calves	14	3 (21.4%)
Subadults	26	3 (11.5%)
Adults	23	0
Total	68	6 (8.8%)

Los Angeles County Museum; Joseph R. Jehl, Jr., San Diego Museum of Natural History; and Charles O. Handley, Jr., U.S. National Museum, kindly made materials in their charge available for study.

LITERATURE CITED

BAER, J. G.
1955. Cestodes d'un dauphin de L'ocean pacifique. Bull. Soc. Neuchatel. Sci. Nat., Ser. 3, 78:33-36.

BARUŠ, V., AND O. COY.
1965. *Freitasia teixeirai* gen. n. et sp. n. and other nematodes parasitizing *Anolis equestris* (Squamata: Iguanidae). Folia Parasitol. (Praha) 15:41-54.

BRODIE, P. F.
1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28:1309-1318.

CALDWELL, D. K., M. C. CALDWELL, W. F. RATHJEN, AND J. R. SULLIVAN.
1971. Cetaceans from the Lesser Antillean Island of St. Vincent. Fish. Bull., U.S. 69:303-312.

DAILEY, M. D., AND R. L. BROWNELL.
1972. A checklist of marine mammal parasites. *In* Mammals of the sea: Biology and medicine, p. 528-589. Charles C. Thomas, Springfield, Ill.

DAVEY, J. T.
1971. A revision of the genus *Anisakis* Dujardin, 1845 (Nematoda: Ascaridata). J. Helminthol. 45:51-72.

DELYAMURE, S. L.
1955. [The helminth fauna of marine mammals in the light of their ecology and phylogeny.] Izd. Akad. Nauk SSSR, Mosk., 517 p. (Translated by Israel Program Sci. Transl., 1968, 522 p.; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-51202).

DOLLFUS, R. P.
1964. A propos de la récolte, à Banyuls d'un cystique de Cestode chez *Tursiops truncatus* (Montagu, 1821). Les cystiques de Cestodes chez les Cétacés et Pinnipèdes. Vie Milieu, Suppl. 17:177-204.

FUHRMANN, O.
1904. Die Tetrabothrien der Säugetiere. Zentralbl. Bakteriol. Parasitenkd. Infektionskr. Hyg. Abt. I Orig. 35:744-752.

JOHNSTON, T. H., AND P. M. MAWSON.
1941. Nematodes from Australian marine mammals. Rec. S. Aust. Mus. Adelaide 6:429-434.

KAGEI, N., T. OSHIMA, A. KOBAYASHI, M. KUMADA, T. KOYAMA, Y. KOMIYA, AND A. TAKEMURA.
1967. Survey of *Anisakis* spp. (Anisakinae, Nematoda) on marine mammals in the coast of Japan. [In Japanese, English summ.] Jap. J. Parasitol. 16:427-435.

KREFFT, G.
1871. On Australian Entozoa, with descriptions of new species. Trans. Entom. Soc. N. S. W. 2:206-232.

MARTIN, W., AND S. ZAM.
1967. *Vasorhabdochona cablei*, gen. et sp. n. (Nematoda) from blood vessels of the marine fish, *Gillichthys mirabilis* Cooper. J. Parasitol. 53:389-391.

MITCHELL, E.
1970. Pigmentation pattern evolution in delphinid cetaceans: An essay in adaptive coloration. Can. J. Zool. 48:717-740.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool. 63:291-370, pl. 27-41.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6):42-45.
1970a. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proc. Sixth Annu. Conf. Biol. Sonar Diving Mammals, p. 45-48.
1970b. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). Zoologica (N.Y.) 54:135-149.
1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish. Bull., U.S. 70:983-1003.

PERRIN, W. F., AND J. R. HUNTER.
1972. Escape behavior of the Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*). Fish. Bull., U.S. 70:49-60.

REYSENBACH DE HAAN, F. W.
1957. Hearing in whales. Acta Otolaryngol., Suppl. 134, 114 p.

RICE, D. W., AND V. B. SCHEFFER.
1968. A list of the marine mammals of the world. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 579, 16 p.

SMITH, W., AND M. B. CHITWOOD.
1967. *Trichospirura leptostoma* gen. et sp. n. (Nematoda: Thelazioidea) from the pancreatic ducts of the white-eared marmoset *Callithrix jacchus*. J. Parasitol. 53:1270-1272.

TOMILIN, A. G., AND M. I. SMYSHLYAYEV.
1968. [Some factors affecting whale mortality (diseases of cetaceans).] Byull. Mosk. O-va. Ispyt. Prir. Otd. Biol. 3:5-12. Transl. in Soviet Studies on Cetaceans, Joint Publ. Res. Serv. Transl. No. 49777, 1970, 19 p. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va.

WILLIAMS, H. H.
1968. The taxonomy, ecology and host-specificity of some phyllobothriidae (Cestoda: Tetraphyllidae), a critical revision of *Phyllobothrium* Beneden, 1849 and comments on some allied genera. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 253:231-307.

YAMADA, M.
1956. An analysis in mass osteology of the false killer whale, *Pseudorca crassidens* (Owen). Part 1. Okajimas Folia Anat. Jap. 28:451-463.

ZAM, S. G., D. K. CALDWELL, AND M. C. CALDWELL.
1971. Some endoparasites from small odontocete cetaceans collected in Florida and Georgia. Cetology 2:1-11.

APPENDIX TABLE 1.—Parasites in *Stenella graffmani*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Terrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balaenae*
CV259	USNM395276	6	1,676	M	3	0	—	0	0	0	2	0	0	0	0	0
CV260	USNM395277	6	1,750	F	4	1	—	0	0	0	0	0	1	3	0	0
CV261	USNM395278	2	1,657	F	3	1	—	0	0	0	0	0	0	2	1	0
CV262	USNM395279	2	1,646	F	3	20	—	0	0	0	1	1	0	0	0	0
CV263	USNM395328	6	1,759	M	3	35	—	0	0	0	0	0	0	5	0	0
CV264	USNM395329	6	1,716	M	3	0	—	0	0	0	2	0	18	7	0	0
CV265	USNM395330	2	1,954	M	4	1	—	0	0	0	4	0	20	26	0	2
CV266	USNM395331	2	1,681	M	3	1	—	0	0	0	0	+	0	2	0	0
CV267	USNM395332	2	1,787	M	4	2		0	0	0	0	0	18	23	0	0
CV268	USNM395333	2	1,900	F	4	4	—	0	0	0	2	0	—	27	0	0
CV269	USNM395334	2	1,837	F	4	2	—	0	0	0	0	0	—	14	0	0
CV270	USNM395336	2	1,815	F	4	0	—	0	0	0	1	0	5	52	0	1
CV271	USNM395337	2	1,821	F	4	8	—	0	0	0	0	0	—	13	0	0
CV272	USNM395338	2	1,850	F	4	0	—	0	0	0	2	0	25	45	0	1
CV273	USNM395339	2	1,630	M	3	61	—	0	0	0	0	0	0	1	0	1
CV274	USNM395385	6	1,782	M	3	0	—	0	0	0	+	0	0	5	0	0
CV275	USNM395386	6	1,570	M	3	2	—	0	0	0	1	0	8	3	0	0
CV276	USNM395387	6	1,578	M	3	16	—	0	0	0	0	0	0	1	0	0
CV277	USNM395388	2	1,816	F	4	8	—	0	0	0	0	0	5	2	0	1
CV278	USNM395389	6	1,632	M	3	18	—	0	0	0	0	0	2	0	0	0
CV279	USNM395390	6	2,183	M	4	8	—	0	0	0	5	0	27	50	2	0
CV280	USNM395391	6	2,032	M	4	14		0	0	0	5	0	32	14	0	0

APPENDIX TABLE 1.—Parasites in *Stenella graffmani*.—*Continued.*

Host						Parasites noted									
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV281	USNM395392	6	1,739	F	3	27	—	0	0	0	+	0	1	1	0	0
CV282	USNM395393	6	1,740	F	3	2	—	0	0	0	2	0	6	4	0	0
CV283	USNM395394	6	2,021	M	4	5	—	0	0	0	13	0	90	28	0	0
CV284	USNM395395	2	1,927	F	4	0	—	0	0	0	0	0	—	—	0	1
CV286	USNM395397	2	1,647	M	3	0	—	0	0	100+	0	0	3	2	2	0
CV287	USNM395417	2	1,732	M	3	0	—	0	0	0	0	0	4	7	0	0
CV289	USNM395594	2	1,767	M	4	0	0	0	0	0	2	0	3	4	0	0
CV290	USNM395595	2	1,627	F	3	0	0	0	0	0	6	0	0	1	0	0
CV291	USNM395596	6	1,927	F	4	1	—	0	0	0	0	0	24	9	0	0
CV292	USNM395597	2	1,895	M	4	5	0	0	34	5	15	0	—	—	0	0
CV293	USNM395598	6	1,996	M	4	2	—	0	0	0	0	0	5	12	0	0
CV295	USNM395527	6	1,390	M	2	9	0	0	0	0	19	0	0	0	1	2
CV296	USNM395528	2	1,298	M	2	0	0	0	0	0	0	+	0	0	0	0
CV297	USNM395529	6	1,429	F	2	2	0	0	0	0	1	0	0	0	0	2
CV298	USNM395530	2	1,540	M	3	4	0	0	0	0	5	+	0	0	0	0
CV300	USNM395532	6	1,438	M	2	11	0	0	0	0	20+	0	0	0	2	2
CV303	USNM395535	6	1,433	M	2	0	0	0	0	0	4	0	0	0	0	0
CV304	USNM395458	2	862	M	1	0	0	0	0	0	0	0	0	0	0	0
CV305	USNM395459	2	780	F	1	0	0	0	0	0	0	0	0	0	0	0
CV306	USNM395460	6	913	M	1	0	0	0	0	0	0	0	0	0	0	0
CV307	USNM395461	2	803	F	1	0	0	0	0	0	0	0	0	0	0	0
CV308	USNM395466	6	793	F	1	0	0	0	0	0	0	0	0	0	0	0
CV309	USNM395463	6	1,878	F	4	9	0	0	0	0	9	0	21	26	0	0
CV310	USNM395464	2	1,801	M	4	3	0	0	0	0	1	0	21	17	0	0
CV311	USNM395465	6	1,995	M	4	4	0	0	0	0	3	0	18	23	0	0
CV312	USNM395462	2	1,640	F	3	7	0	0	0	0	0	0	1	0	0	0
CV313	USNM395467	2	1,601	M	3	8	0	0	0	0	5	0	0	2	0	0
CV314	USNM395468	2	1,842	F	4	1	0	0	0	0	0	0	+	+	0	0
CV315	USNM395603	2	1,621	M	3	7	+	0	0	0	12	0	3	5	0	0
CV316	USNM395604	2	1,679	M	3	12	0	0	0	0	0	0	1	4	0	0
CV317	USNM395605	2	1,375	M	2	7	0	0	0	0	5	0	0	0	0	2
CV318	USNM395606	2	1,444	F	2	8	0	0	0	0	0	0	0	0	0	0
CV319	USNM395607	6	1,681	F	3	2	0	0	0	0	1	0	5	0	0	0
CV320	USNM395608	2	1,670	M	3	20	+	0	0	0	13	0	7	0	0	0
CV321	USNM395609	2	1,525	M	3	1	0	0	0	0	0	0	1	0	0	0
CV322	USNM395610	6	1,423	F	2	9	0	0	0	0	6	0	0	0	0	0
CV323	USNM395611	2	1,617	M	3	5	0	0	0	0	0	0	4	2	0	0
CV324	USNM395612	6	1,356	F	2	0	0	0	0	0	13	0	+	0	0	0
CV325	USNM395613	6	1,348	M	2	4	+	0	0	0	8	0	1	0	2	2
PQ01	USNM395407	lat ~8°N, long 107°W	1,978	M	4	3	—	0	0	0	0	0	5	18	0	0
PQ02	USNM395408	lat ~8°N, long 107°W	1,590	M	2	7	—	0	0	0	0	+	0	0	0	0
[4]PQ04	USNM395410	lat ~8°N, long 107°W	1,677	F	3	3	—	0	0	0	0	0	2	8	1	0
WFP10	CAS15662	lat ~14°N, long 100°W	1,865	F	4	11	—	0	0	0	0	0	—	—	0	0
WFP11	UCMP86284	lat ~14°N, long 99-108°W	1,304	M	2	—	+	—	—	—	—	+	—	—	—	—
WFP12	MVZ140640	lat ~14°N, long 100°W	1,671	M	3	—		—	—	—	—	0	—	—	—	—
WFP13	UCMP23071	lat ~10°N, long 100°W	1,572	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP19	CAS15663	lat ~10°N, long 100°W	1,536	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP20	MVZ140643	lat ~10°N, long 100°W	1,708	F	3	—	0	—	—	—	—	—	—	—	—	—
WFP3	LACM37549	lat 14°30′N, long 99° 10′W	1,252	F	2	0	0	0	0	0	2	0	0	0	0	2
WFP4	LACM37550	lat 14°30′N, long 99° 10′W	1,260	M	2	0	0	0	0	0	0	0	0	0	0	0

[1] CAS = California Academy of Sciences, San Francisco
LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51′N, long 93° 18′W
Locality for collection number 6: lat 7°11′N, long 90°32′W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

[4] This specimen also infected with *Crassicauda*.

APPENDIX TABLE 2.—Parasites in *Stenella* cf. *S. longirostris*.

Host						Parasites noted									
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilacephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balaenae*
CV285	USNM395396	2	1,769	F	4	56	—	0	50+	50+	3	0	27	13	2	0
CV288	USNM395593	6	1,726	F	4	2	—	0	—	—	—	—	+	+	—	—
CV294	USNM395526	6	1,494	F	2	1	+	0	0	0	10	0	8	0	1	0
CV299	USNM395531	2	1,189	M	2	4	0	0	0	0	5	0	0	0	0	4
CV301	USNM395533	2	1,396	F	2	0	0	0	0	0	0	0	0	0	2	0
CV302	USNM395534	2	1,184	M	2	9	0	0	0	0	20+	0	0	0	0	1
PQ03	USNM395409	lat ~8°N, long 107°W	1,571	F	3	8	0	0	0	0	8	0	8	2	2	6
PQ05	USNM395411	lat ~8°N, long 107°W	1,680	F	4	5	—	0	0	0	0	0	13	13	0	0
PQ06	USNM395412	lat ~8°N, long 107°W	1,729	F	4	9	—	1	0	0	0	0	0	4	1	0
PQ07	USNM395413	lat ~8°N, long 107°W	1,761	F	4	9	—	0	0	0	0	0	8	6	1	0
PQ08	USNM395414	lat ~8°N, long 107°W	1,734	M	4	1	—	0	0	0	2	0	7	17	0	0
PQ09	USNM395599	lat ~8°N, long 109°45'W	1,727	M	4	1	0	0	0	0	0	0	21	8	1	2
PQ10	USNM395600	lat ~8°N, long 107°W	1,086	F	2	7	—	0	0	0	0	0	0	0	0	1
PQ11	USNM395601	lat 8°N, long 109°45'W	1,054	F	2	0	—	0	0	0	6	+	0	0	0	1
WFP14	CAS15664	lat ~14°N, long 99-108°W	1,618	F	4	—	+	—	—	—	—	—	—	—	—	—
WFP15	CAS15665	lat ~14°N, long 100°W	1,637	M	4	—	+	—	—	—	—	—	—	—	—	—
WFP21	MVZ140641	lat ~14°N, long 100°W	1,651	M	3	—	+	—	—	—	—	—	—	—	—	—
WFP22	CAS15668	lat ~10°N, long 100°W	1,750	M	4	—	—	—	—	—	—	—	—	—	—	—
WFP6	LACM37551	lat 10°40'N, long 108°40'W	896	F	2	0	0	0	0	0	0	0	0	0	0	0

[1] CAS = California Academy of Sciences, San Francisco
LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51'N, long 93°18'W
Locality for collection number 6: lat 7°11'N, long 90°32'W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

VERTICAL DISTRIBUTION PATTERNS OF GOLDEYE, *HIODON ALOSOIDES*, IN FORT PECK RESERVOIR, MONTANA

JAMES L. COOPER[1]

ABSTRACT

In November 1967 and continuing into December 1969, the goldeye, *Hiodon alosoides* (Rafinesque), in Fort Peck Reservoir, Mont., exhibited seasonal vertical distribution patterns, which seemed to be related to the surface-water temperature. When surface-water temperatures were above 8.9°C (summer and early fall), the goldeye congregated near the surface. During the late fall, ice-covered period, and spring when surface temperatures varied between 8.9° and 1.1°C, the goldeye usually congregated between the 8- and 32-ft level. However, it is the opinion of the author that the goldeye were following the food source and were not responding to temperature per se.

The goldeye, *Hiodon alosoides* (Rafinesque), is one of two shadlike freshwater fishes belonging to the Family Hiodontidae. Distribution of goldeye is limited in the United States and Canada (found mostly in the prairie States and Provinces). The goldeye is generally described as being found in shallow, turbid lakes and large river systems (Battle and Sprules, 1960; Kennedy and Sprules, 1967) and in the shallow waters of large lakes (Kennedy and Sprules, 1967). However, Bajkov (1930) observed that goldeye were found on the surface over deep water in Lake Winnipeg, Manitoba, and Borges (1950) netted goldeye in the deep water of the Lake of the Ozarks, Mo., in September.

Fort Peck Reservoir is basically a deep, clear body of water in contrast to the lakes generally described as being inhabited by goldeye. However, goldeye were netted during 1966 in quantity on the surface in clear water. Good numbers of goldeye continued to be netted in clear water during 1967-70 (unpublished data available in annual report form of Montana Fish and Game Department).

Mature goldeye often exceed 15 inches in total length in nutrient-rich bodies of water; the Montana record is 18.7 inches total length (Brown, 1971) and was taken from Nelson Reservoir, a fertile lake about 70 miles from Fort Peck Reservoir. In Fort Peck Reservoir, the goldeye rarely exceeded 15 inches in total length and most were less than 14 inches total length; they seldom lived longer than 8 years; most spawned in June; and they withstood water temperatures as low as 1.1°C (unpublished data).

The coho salmon, *Oncorhynchus kisutch*, which was first introduced in 1969, was the only species to compete with goldeye for food in pelagic areas of the reservoir. In shallow-water areas, the goldeye contributed to the diets of sauger, *Stizostedium canadense*; walleye, *S. vitreum vitreum*; and northern pike, *Esox lucius* (personal observations).

The goldeye is one of the most important commercial fish taken from the reservoir. The goldeye are trucked to Winnipeg, Manitoba, which has the only substantial commercial market (up to 1 million lb of drawn fish are utilized annually). However, it has only been since 1967 that the market for goldeye from Fort Peck Reservoir has been significant. Declining populations of goldeye in Canadian waters, probably due to overharvesting by commercial fishermen, were responsible for the interest in Fort Peck Reservoir's goldeye (goldeye harvest from Fort Peck Reservoir varied from 53,318 to 199,279 lb round weight during 1967-71). See Battle and Sprules (1960), Grosslein and Smith (1959), and Kennedy and Sprules

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(1967) for a past history of the commercial fishery in Canada and the United States.

To better understand the problems associated with harvesting goldeye from the clear waters of Fort Peck Reservoir, the availability of goldeye to gill net fishermen at different times of the day and year was investigated. Emphasis was placed on selective fishing; i.e., floating gill nets, 8 ft deep, were set in open-water areas away from shallow bays and shorelines to avoid game fish. The results of selective netting revealed that goldeye were present in commercial quantity away from shallow, turbid areas and that the catch consisted of almost 100% goldeye (unpublished data).

However, during the winter, spring, and late fall, the goldeye were not gilled in the floating gill nets. Preliminary netting with 8-ft-deep, sinking gill nets (nets were set obliquely and horizontally at different depths) indicated that the goldeye were present during the fall and spring periods, but usually at the 20- to 30-ft level. To better determine some of the parameters associated with the vertical distribution of goldeye, the following study was begun in November 1967.

DESCRIPTION OF FORT PECK RESERVOIR AREA AND SAMPLING SITE

Fort Peck Reservoir is located in sparsely populated northeastern Montana. At maximum pool the reservoir has a surface area of 245,000 acres, a maximum depth of 225 ft near the dam, and an irregular shoreline over 1,500 miles long. Only the Missouri River and Musselshell River continuously flow into the reservoir. There are detailed descriptions of the area (U.S. Fish and Wildlife Service, 1952).

The water of the reservoir is clear except for the shallow ends of large bays and upper ends of the two main arms (Missouri Arm formed by the Missouri River and the Big Dry Arm formed by the intermittent Big Dry Creek). Surface-water temperatures varied from freezing in winter (the Reservoir is completely ice-covered for almost 4 mo) to the low 20°C in summer.

There was little indication of thermal stratification. During the ice-cover period, the water temperature in the sampling area was 1.1°C from the surface to at least a depth of 50 ft. Also, water tapped from approximately 140 to 160 ft below the surface for the turbines at the dam was 1.1°C during most of the above period (records kept by U.S. Corps of Engineers at Fort Peck). The continued withdrawal of water for power production (10,000 cfs) probably discouraged formation of a winter inverse stratification. The almost ever present prairie winds and withdrawal of water for power production probably discouraged the formation of a true summer thermocline. During the warm months of July and August, the temperature from the surface to depth of 50 ft varied only a few degrees Celsius in the sampling area. Phenicie (1950) found little evidence of a thermocline, and he recorded a high temperature of 8.3°C at a depth of 180 ft. Temperature data kept by the U.S. Army Corps of Engineers during July and August were usually in the 9°-13°C range for water taken from the 140- to 160-ft level.

The area sampled was open water located from ½ to 1 mile off a point of land near the west end of Fort Peck Dam. The water was clear, and depths ranged from 50 ft to over 100 ft. Netting efforts in other parts of the lower reservoir area by the Montana State Fish and Game Department and commercial fishermen indicated that the sampling site was representative of open, clear-water areas of the lower reservoir.

MATERIALS AND METHOD

To determine the vertical distribution of the goldeye, a floating nylon gill net was used. The net measured 100 ft long and 40 ft deep. The webbing, of No. 139 nylon twine, was 1½-inch mesh, square measure. The net was divided into five horizontal sections, each 8 ft deep. The depth of 40 ft was chosen since numerous (approximate number not known) test-netting efforts during spring, summer, and fall of 1966-69 gilled few goldeye below the 40-ft depth (oblique, horizontal, and bottom sets were utilized). Most of the Montana State Fish and Game Department and commercial

fishery goldeye nets have No. 139 nylon twine. This 1½-inch mesh was selected because it gilled more goldeye than 1-inch, 1¼-inch, 1¾-inch, or 2-inch mesh (unpublished data). Eight-foot sections represented the width of gill nets used for goldeye on the Reservoir.

Usually the net was set for overnight and then lifted. It was observed that daylight sets rarely caught many goldeye in clear water. The exact time of setting and lifting the net usually had little influence on the catch as long as the net was set well before dusk and lifted after sunrise. Because so few goldeye were caught in overnight sets during the ice-cover period in 1968, the net was set for several days before lifting during the 1969 ice-cover period.

RESULTS

The vertical distribution pattern can be followed in Table 1.

During the summer and early fall, the goldeye exhibited maximum stratification within 8 ft of the surface, and they were easily captured by floating gill nets. The summer and early fall pattern began in 1968 and 1969 once the surface temperature reached 7.2°C and remained above 13.3°C.

The late fall pattern in 1967, 1968, and 1969 eventually exhibited the reverse of the summer pattern; i.e., the greatest concentration in the top 40 ft was between the 32- and 40-ft level. However, the goldeye did not move quickly from the surface to deeper depths. There was a transitional period during which the goldeye were scattered throughout all depths sampled (0-40 ft). The late fall pattern began as the surface temperature approached 6.1°C in 1967 and 8.9°C in 1968 and 1969.

During the ice-cover period, the goldeye appeared to concentrate between the 8- and 32-ft level; however, few goldeye were taken per night set. In 1968, the catch per night set was 22 goldeye; in 1969, the equivalent catch per night set was 3.5 goldeye. In contrast, the ice-free period usually had catches of 60 or more goldeye per night set. The water temperature was 1.1°C both winters.

The goldeye vertical distribution pattern in the spring was not as predictable as in other periods. The goldeye were caught at all depths, near the surface, or near the 40-ft depth. No clear relationship between the distribution pattern and temperature was evident. Apparently quick shifts in wind direction affected surface temperatures more in spring than in summer and fall. Since the warm surface-water column in summer and fall penetrated to deeper levels than the spring warm surface column, maybe upward convection currents more easily displaced surface water in the spring.

DISCUSSION

The following discussion concerns mostly the open-water area; i.e., little reference is made to the goldeye that may habitually seek shallow, turbid conditions such as would be found in small bays and near river mouths.

It is evident that the goldeye in the sampling area do exhibit consistent seasonal vertical distribution patterns and that the patterns can usually be predicted from the surface-water temperature. The cause of the patterns is not clear, but it is suspected that the goldeye is following the food source, which in Fort Peck Reservoir consists of zooplankton, terrestrial insects, aquatic insects, and small fishes. It is believed from observations (regurgitation of stomach contents when goldeye were forced through the mesh), daytime versus night-time sets, and cursory stomach examinations that the goldeye do most of their feeding at night during the summer and early fall when zooplankton and terrestrial and emergent aquatic insects are available on or near the surface. Work by Bajkov (1930) and Grosslein and Smith (1959) support the above contention as does work by Sprules (1947).

It is not known whether the goldeye move to deeper water during the day. Surface sets over clear, deep water during the day have caught few goldeye although sets in turbid, shallow areas often produce substantial catches. Possibly the fish gilled in the shallow, turbid water could not see the net.

Obviously, terrestrial insects do not contribute significantly to the diet during the

TABLE 1.—Vertical distribution pattern of goldeye in an open-water area of Fort Peck Reservoir, from November 1967 into December 1969.

[Number of goldeye per night per 8-ft deep section of 100-ft net.]

Pattern	Date	Temperature (°C)[1]	Depth (ft) 0-8	8-16	16-24	24-32	32-40
1967							
Summer-early fall	20 Nov.	8.9	48	28	7	1	0
	24 Nov.	7.8	66	56	22	4	2
Late fall	5 Dec.	6.1	18	46	51	40	52
	16 Dec.	4.4	1	6	26	25	44
1968							
Winter ice-cover	17 Jan.	1.1	0	9	14	6	3
	9 Feb.	1.1	4	14	8	2	0
	15 Feb.	1.1	2	0	1	0	0
	16 Feb.	1.1	2	3	0	1	0
	23 Feb.	1.1	0	13	1	0	0
	1 Mar.	1.1	0	4	7	0	0
Spring	11 Apr.	2.8	1	7	9	6	2
	19 Apr.	3.2	14	31	47	41	25
	23 Apr.	3.2	2	6	5	4	0
	24 Apr.	7.2	6	17	16	11	7
	25 Apr.	3.9	20	11	3	1	3
	1 May	5.0	86	82	86	57	40
	12 May	6.1	11	10	15	6	15
Summer-early fall	20 May	7.2	21	14	13	10	16
	24 May	8.3	12	4	2	5	3
	6 June	12.2	41	39	38	20	20
	13 June	13.3	41	8	5	6	6
	26 June	15.6	75	35	18	18	18
	17 July	19.4	37	8	11	3	3
	25 July	18.7	38	7	5	2	2
	6 Aug.	20.0	51	18	3	5	5
	27 Aug.	17.8	61	19	15	13	22
	4 Sept.	17.2	26	10	17	14	6
	10 Oct.	14.4	34	26	16	7	10
	23 Oct.	12.8	86	79	19	10	10
	12 Nov.	10.6	37	35	9	13	6
Late fall	22 Nov.	8.9	15	21	26	11	9
	3 Dec.	7.2	5	20	20	29	8
	10 Dec.	6.1	0	12	18	14	18
	18 Dec.	5.0	0	9	21	50	57
1969							
Winter ice-cover	15 Jan.	1.1	0	6	15	20	9
	6 Feb.	1.1	0	0	1	0	0
	6-10 Mar.	1.1	0	1	2	0	0
	10-13 Mar.	1.1	1	5	1	2	0
	13-18 Mar.	1.1	2	2	7	1	0
	18-25 Mar.	1.1	1	2	6	2	0
	25 Mar.-3 Apr.	1.1	1	9	1	3	0
	3-7 Apr.	1.1	2	5	4	5	0
Spring	22-24 Apr.	2.8	12	14	28	17	19
	1 May	3.3	0	1	3	4	3
	8 May	3.9	24	9	6	14	15
	14 May	8.3	63	9	8	6	8
	21 May	7.2	3	8	5	5	11
	29 May	6.7	18	26	22	8	8
	6 June	14.4	77	11	7	10	9
	13 June	7.8	19	26	6	5	3

TABLE 1.—Vertical distribution pattern of goldeye in an open-water area of Fort Peck Reservoir, from November 1967 into December 1969.—Continued.

[Number of goldeye per night per 8-ft deep section of 100-ft net.]

Pattern	Date	Temperature (°C)[1]	Depth (ft) 0-8	8-16	16-24	24-32	32-40
1969 — Continued							
Summer-early fall	20 June	13.3	52	24	26	12	5
	11 July	16.7	110	77	39	21	21
	16 July	[2]	27	6	8	10	5
	23 July	17.2	46	14	5	2	1
	27 Aug.	21.1	46	21	25	6	4
	18 Sept.	[2]	60	45	40	16	12
	9 Oct.	15.0	55	35	19	1	4
	22 Oct.	[2]	25	23	17	9	7
	30 Oct.	10.6	21	11	5	1	2
	5 Nov.	11.1	19	15	3	8	5
	15 Nov.	9.4	23	11	4	2	2
Late fall	19 Nov.	8.9	10	20	11	8	6
	21 Nov.	8.3	6	21	20	9	1
	26 Nov.	7.8	8	9	3	2	7
	9 Dec.	5.6	0	1	16	21	35

[1] Taken at surface.
[2] Temperature not known.

late fall, winter, and early spring. Cursory examination of stomachs and observation of regurgitated materials during the above periods showed that goldeye preyed almost exclusively on cladocerans.

To better understand if goldeye in fact follow the food source during the late fall, winter, and early spring, the seasonal vertical distribution patterns of cladocerans would have to be known. Although no studies have been conducted to establish distribution patterns of Fort Peck Reservoir zooplankton, work by other investigators indicated that many zooplankters exhibit seasonal vertical migratory patterns. Accordingly, the season migrations are not necessarily hydrographic (McLaren, 1963), but it has been suggested by some authors that winter hibernation of zooplankton may just be an interruption of diurnal rhythm; i.e., once the body of water cools to a given temperature, diurnal movement is no longer advantageous and ceases. Possibly, the goldeye is browsing on zooplankton which have ceased to exhibit diurnal movement patterns similar to their summer pattern, thus accounting for the late fall, winter, and spring distribution patterns exhibited by the goldeye.

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LITERATURE CITED

BAJKOV, A.
1930. Fishing industry and fisheries investigations in the prairie provinces. Trans. Am. Fish. Soc. 60:215-237.

BATTLE, H. I., AND W. M. SPRULES.
1960. A description of the semi-buoyant eggs and early development stages of the goldeye, *Hiodon alosoides* (Rafinesque). J. Fish. Res. Board Can. 17:245-266.

BORGES, H. M.
1950. Fish distribution studies, Niangua Arm of the Lake of the Ozarks, Missouri. J. Wildl. Manage. 14:16-23.

BROWN, C. J. D.
1971. Fishes of Montana. Big Sky Books, Mont. State Univ., Bozeman, 207 p.

GROSSLEIN, M. D., AND L. L. SMITH, JR.
1959. The goldeye *Amphiodon alosoides* (Rafinesque), in the commercial fishery of the Red Lakes, Minnesota. U.S. Fish Wildl. Serv., Fish. Bull. 60:33-41.

KENNEDY, W. A., AND W. M. SPRULES.
1967. Goldeye in Canada. Fish. Res. Board Can., Bull. 161, 45 p.

MCLAREN, I. A.
1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J. Fish Res. Board Can. 20:685-727.

PHENICIE, C. K.
1950. The Fort Peck Reservoir Fishery Survey. Prog. Rep. Mont. Fish Game Comm., Bull. 3, 19 p.

SPRULES, W. M.
1947. A management program for goldeye (*Amphiodon Alosoides*) in Manitoba's marsh regions. Can. Fish Cult. 2:9-11.

U.S. FISH AND WILDLIFE SERVICE.
1952. A three-year fishery investigation, Fort Peck Reservoir. U.S. Fish Wildl. Serv., Missouri River Basin Studies, 49 p.

A MERISTIC AND MORPHOMETRIC COMPARISON OF THE HAKES, *UROPHYCIS CHUSS* AND *U. TENUIS* (PISCES, GADIDAE)[1, 2]

J. A. MUSICK[3]

ABSTRACT

Urophycis chuss and *U. tenuis* are shown to be statistically different for several meristic and morphometric characters. The ranges of the number of lateral line scales are distinct, *U. chuss* having 95 to 117 and *U. tenuis* having 119 to 148. The numbers of gill rakers on the epibranchial of the first gill arch are distinct, *U. chuss* having three and *U. tenuis* having two. The number of abdominal vertebrae and the regression of head length on standard length can be used to distinguish between the two species, with certain reservations. Two characters previously used in the literature to distinguish between the two species are not valid. These are: the relation of upper jaw length to the distance from the snout to the posterior margin of the orbit, and the relation of the distance from the origin of the pelvic fin to the anus to the length of the pelvic fin. Samples of *U. tenuis* from off New England and Nova Scotia appear to be morphometrically different from those from the Gulf of St. Lawrence.

The genus *Urophycis* Gill (1963) includes at least seven species of gadid fishes endemic to the western Atlantic Ocean (Svetovidov, 1948:105). The most abundant of these in the area north and east of Delaware Bay are *U. chuss* (Walbaum, 1792) and *U. tenuis* (Mitchill, 1814) which are difficult to distinguish (Figures 1 and 2). These two species have been repeatedly confused since *U. tenuis* was first described by Mitchill (1814), who recognized the meristic differences between them but apparently did not always recognize the species by sight, because he gave the maximum weight for *Gadus longipes* (= *U. chuss*) as 18 lb. *U. chuss* rarely, if ever, exceeds 6 lb, whereas *U. tenuis* may reach 40 lb or more, and often exceeds 18 lb (Musick, 1969). Among the long list of confused and misnamed accounts in the literature, the outstanding ones are Rafinesque-Schmaltz (1818), Storer (1839), Kaup (1858), Cornish (1907, 1912), and Vladykov and McKenzie (1934) who placed *U. tenuis* within the synonymy of *U. chuss*, after a "study of the literature."

Both *U. tenuis* and *U. chuss* are taken commercially throughout their ranges. The International Commission for the Northwest Atlantic Fisheries (ICNAF) has the responsibility of reporting the annual catch statistics for all major species, including *U. chuss* and *U. tenuis*, taken in the ICNAF area. Musick (1967)[4] pointed out that the statistics for *Urophycis* frequently were in error because of misidentification. Recently, Leim and Scott (1966:217) were compelled to discuss the biology, distribution, and commercial value of *U. chuss* and *U. tenuis* together because of the confused treatment of species in earlier Canadian literature.

The purpose of this paper is to test the validity of certain characters previously used in the literature to distinguish between *U. chuss* and *U. tenuis* and to examine additional characters of potential diagnostic value. Seven

[1] Virginia Institute of Marine Science Contribution No. 518.

[2] Based on part of a doctoral dissertation presented to Harvard University.

[3] Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[4] Musick, J. A. 1967. Designation of the hakes, *Urophycis chuss* and *U. tenuis* in I.C.N.A.F. statistics. Int. Comm. Northwest Atl. Fish., Res. Doc. 67-76, No. 1872, 5 p. (Unpubl.)

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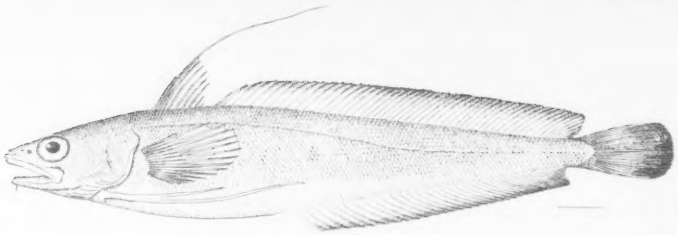

FIGURE 1.—*Urophycis chuss*, drawing from USNM 28707, courtesy of the Smithsonian Institution.

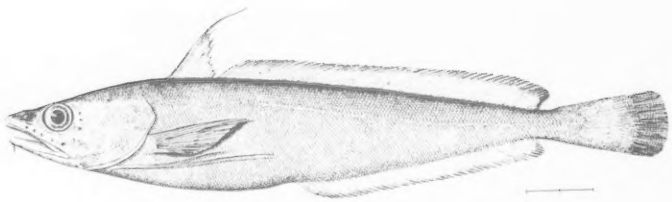

FIGURE 2.—*Urophycis tenuis*, drawing from USNM 21029, courtesy of the Smithsonian Institution.

meristic and 10 morphometric characters were examined on 136 *U. chuss* and 170 *U. tenuis*. Six meristic and four morphometric characters were chosen for statistical analysis.

METHODS

All samples were taken between the Gulf of St. Lawrence and the Virginia coast (Figure 3 and Appendix Table). Preliminary studies suggested that *Urophycis* of the *chuss-tenuis* complex from the study area could be readily placed into two morphs by body shape and scale size, thicker-bodied, small-scaled individuals being similar to published descriptions of *U. tenuis* and slim-bodied, larger-scaled specimens resembling descriptions of *U. chuss*. Thus specimens were tentatively identified. *U. tenuis* was present in the entire sampling area, whereas with the exception of a few Nova Scotian shelf specimens *U. chuss* was found in the Gulf of Maine and south and west of there. Samples of *U. tenuis* were available, by chance, from three geographic areas: the Gulf of Maine and southern New England waters (N.E.), the eastern coast of Nova Scotia from the vicinity of Halifax to the north and east (N.S.), and the Northumberland Straits in the Gulf of St. Lawrence adjacent to Prince Edward Island (P.E.I.). This geographic segregation of samples was maintained for statistical analyses because *U. tenuis* was predominant in Canadian waters where the species of *Urophycis* have been regarded with confusion for many years, especially in the Gulf of St. Lawrence. The data from all specimens of *U. chuss* were treated as one statistical sample.

Length in the rest of this paper refers to standard length unless designated otherwise. Specimens 50 mm long or less were cleared and stained following a method modified from Hollister (1934) to count the number of fin rays, gill rakers, and vertebrae. Fin rays on larger specimens were counted with the aid of a fine needle and occasionally by x-ray examination. All radiographs were taken on Picker "Pictronix 200"[5] x-ray equipment, using Gevaert D7 Structurix Industrial x-ray Safety Film (Unipac), and developed by the procedure outlined by Bartlett and Haedrich (1966). Vertebral numbers on specimens longer than 50 mm were determined from radiographs and, in two instances, by dissection. Lateral line scale rows were counted from a point directly above the upper corner of the opercular opening to the base of the midcaudal ray.

All measurements taken from specimens

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

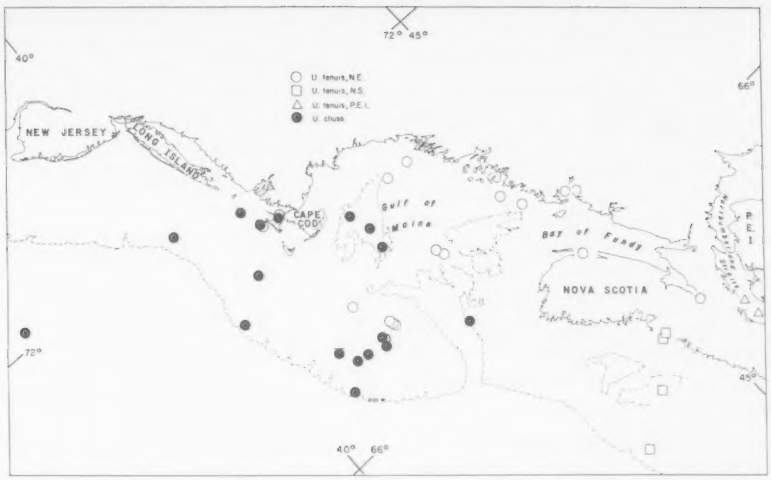

FIGURE 3.—Localities where *Urophycis* were collected for a study of meristics and morphometrics. *U. chuss* was compared with samples of *U. tenuis* from New England (N.E.), Nova Scotia (N.S.), and the Gulf of St. Lawrence (P.E.I.).

smaller than about 600 cm were made with fine-pointed dividers. Larger specimens were measured with calipers consisting of a meter stick and sliding brass "jaws." When possible, measurements were made on the left side of the specimens.

The number of fin rays in the second dorsal fin and in the anal fin, the number of abdominal vertebrae, and the total number of vertebrae were each subjected to an analysis of variance (Snedecor, 1956:246). Abdominal vertebrae are those anterior to the caudal vertebrae. An analysis of variance of the number of lateral line scales was performed only among the three samples of *U. tenuis* because the ranges of variation of *U. chuss* and *U. tenuis* do not overlap. The gill rakers were counted on the epibranchial of the first gill arch. The raker found at the joint between the epibranchial and ceratobranchial was not included in the count.

The meristic data have been summarized in Figures 4 to 8, and the method of graphing follows that of Hubbs and Hubbs (1953). For each sample the range of variation is shown by a heavy horizontal line, the mean ($\bar{x}$) by a small narrow triangle. The blackened part of each bar comprises two standard errors of the mean ($2s_{\bar{x}}$) on either side of $\bar{x}$. One-half of each black bar, plus the white bar at either end, outline one standard deviation (s) on either side of $\bar{x}$; s indicates dispersion; $2s_{\bar{x}}$, reliability of $\bar{x}$.

Tests of significance were performed at the 1% level, and if no difference was found, at the 5% level. Statistical significance is designated as follows: NS = not significant; * = significant at the 5% level; ** = significant at the 1% level. If significance was found, Duncan's Multiple Range Test was conducted at the 1% and 5% probability levels (Duncan, 1955, 1957). The results of Duncan's test include within the same parentheses those samples which are not significantly different.

The effect of allometric variation on character validity in *Urophycis* has not been considered in the past. In the present study, an attempt was made to measure specimens of all sizes. All values were transformed to logarithms to reduce the correlation between the variance and the mean (Mottley, 1941), and regressions were computed for each character for each of the four samples. Every sample was tested against each of the others by an analysis of covariance (Steel and Torrie, 1960). Variances were tested for homogeneity. Hetero-

geneous variances in most instances could be attributed to disparities between the ranges of the independent variables of the regressions. Elimination of high or low independent values from one or both regressions usually resulted in homogeneity. When the variances were heterogeneous and the ranges of independent variables were about the same in both regressions, heterogeneity was attributed to intrinsic properties within the samples and they were considered significantly different. If the variances of the regressions were homogeneous, the analysis of covariance was continued and the slopes were tested. The adjusted means were tested if the slopes were not significantly different at the 1% level.

Analyses of covariance were performed between males and females in each sample before interarea comparisons were attempted. No sexual dimorphism was found.

Bigelow and Schroeder (1953:222) contended that the position of the rear of the upper jaw, relative to the position of the eye, was a dependable character for separating *U. chuss* from *U. tenuis*. This character may not be reliable because the position of the rear edge of the maxillary depends on the extent to which the mouth of the fish is open. A more accurate method of quantifying the character was used in this study. The distance from the snout to the posterior margin of the maxillary (upper jaw length) was compared to the distance from the snout to the posterior margin of the orbit. A second morphometric character used by many authors to distinguish between *U. chuss* and *U. tenuis* is the length of the ventral fin relative to the position of the anus. However, Bigelow and Schroeder (1953), Goode and Bean (1895), and others have pointed out that this character may not be dependable. An analysis was made of the regression of ventral fin length on the distance from the origin of the ventral fin to the anus.

Subjective observations suggest that *U. tenuis* has a larger head and forebody than *U. chuss*. Therefore, regression analyses were made of the preanal length and head length on standard length. Hubbs and Lagler (1958:25) advocate measuring head length from the tip of the snout to the "most distant point of the opercular membrane," which may vary, depending on whether the fish's operculum is expanded or closed tightly against the head. Head length is defined here as the distance from the tip of the snout to the upper, inner angle of the opercular opening. Preanal length is defined here as the distance from the tip of the snout to the anus.

RESULTS

Meristic Analysis

Number of Rays in Second Dorsal and Anal Fins and of Abdominal Vertebrae (Figures 4-6)

The statistical analyses for these three characters yielded the same results for all comparisons. The analysis of variance showed heterogeneity at the 1% level, and the Duncan's test separated all samples of *U. tenuis* from *U. chuss*. There were no significant differences among the samples of *U. tenuis*.

Total Number of Vertebrae (Figure 7)

Heterogeneity of variance was shown at the 1% level. Duncan's test showed significant differences between *U. chuss* and both *U. tenuis* N.E. and *U. tenuis* P.E.I. However, there were no significant differences between *U. chuss* and *U. tenuis* N.S., nor among the samples of *U. tenuis*.

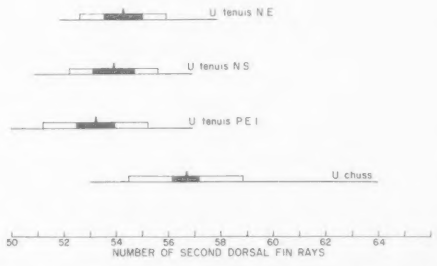

FIGURE 4.—Comparison of the number of rays in the second dorsal fin among three samples of *Urophycis tenuis* and one of *U. chuss*. Range—horizontal line. Mean ($\bar{x}$)—small narrow triangle. Two standard errors of the mean on either side of $\bar{x}$—blackened part of each bar. One standard deviation on either side of $\bar{x}$—one-half of each black bar, plus the white bar at either end.

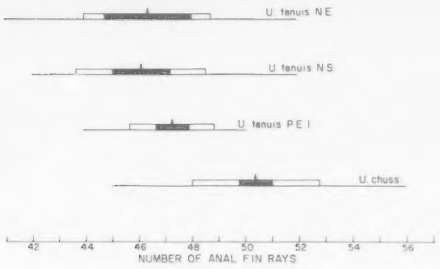

FIGURE 5.—Comparison of the number of rays in the anal fin among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

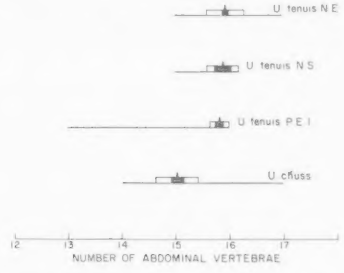

FIGURE 6.—Comparison of the number of abdominal vertebrae among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

Number of Lateral Line Scales (Figure 8)

The ranges of variation of the two species did not overlap. There were no significant differences among the samples of *U. tenuis*.

Number of Gill Rakers on the Epibranchial

The gill rakers of 56 *U. chuss* and 111 *U. tenuis* were counted. All *U. chuss* had three gill rakers on the epibranchial, and all *U. tenuis* had two.

Morphometric Analysis

Regression of Distance from Snout to Posterior Margin of Orbit on Upper Jaw Length (Figure 9, Table 1)

All regressions were linear. *U. tenuis* N.S.

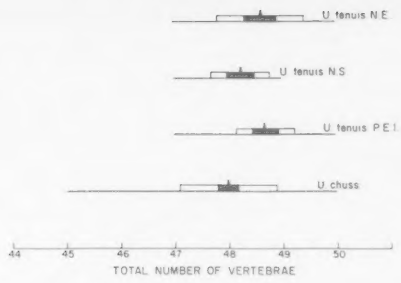

FIGURE 7.—Comparison of the number of vertebrae among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

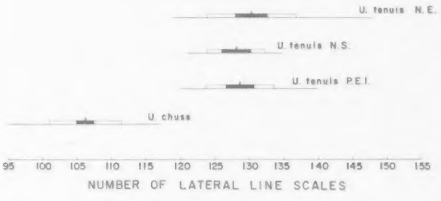

FIGURE 8.—Comparison of the number of lateral line scales among three samples of *Urophycis tenuis* and one of *U. chuss*. Explanation of parts of the graph is given in Figure 4 legend.

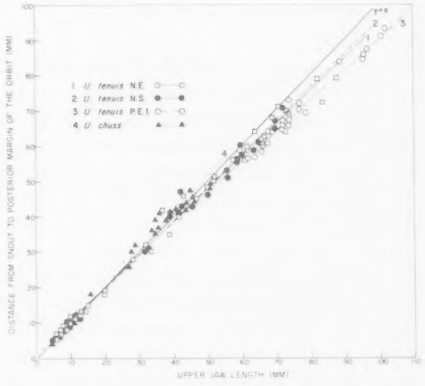
1. U. tenuis N.E.
2. U. tenuis N.S.
3. U. tenuis P.E.I.
4. U. chuss
DISTANCE FROM SNOUT TO POSTERIOR MARGIN OF THE ORBIT (MM)
UPPER JAW LENGTH (MM)

FIGURE 9.—Regression of the distance from the snout to the posterior margin of the orbit on upper jaw length from three samples of *Urophycis tenuis* and one of *U. chuss*.

TABLE 1.—Summary of all morphometric comparisons of *Urophycis tenuis* and *U. chuss*.

	U. tenuis[1]		*U. chuss*
	N.S.	P.E.I.	
U. tenuis:			
N.E.:[2]			
a.	NS	*	**
b.	*	—	**
c.	NS	**	**
d.	NS	*	**
N.S.:			
a.		NS	*
b.		—	**
c.		NS	**
d.		**	**
P.E.I.:			
a.			NS
b.			—
c.			**
d.			*

[1] N.S. = eastern coast of Nova Scotia from vicinity of Halifax to north and east.
P.E.I. = Northumberland Straits in Gulf of St. Lawrence adjacent to Prince Edward Island.
NS = not significant.
* = significant at 5% level.
** = significant at 1% level.
[2] N.E. = Gulf of Maine and southern New England waters.
Regression of:
a. distance from snout to posterior margin of orbit on upper jaw length.
b. length of pelvic fin on distance from origin of pelvic fin to anus.
c. head length on standard length.
d. preanal length on standard length.

was not significantly different from *U. tenuis* N.E. or P.E.I. Regression coefficients for the latter two samples were significantly different at the 5% level. The adjusted mean for *U. chuss* was significantly different from that of *U. tenuis* N.E. at the 1% level and from that of *U. tenuis* N.S. at the 5% level. No significant differences were found between *U. chuss* and *U. tenuis* P.E.I.

The contention of Bigelow and Schroeder (1953:223), that this character "can be relied on, even for very small fish," is not borne out. If true, all values of *U. tenuis* would be on or to the right of the line $y = x$, and those for *U. chuss* would be to the left of the line (Figure 9).

Regression of Length of Pelvic Fin on Distance from Origin of the Pelvic Fin to Anus (Figure 10, Table 1)

This relationship was linear for *U. chuss*, but the values for *U. tenuis* seemed to be curvilinear. The slope of the regression changed when the independent variable reached 150 to 160 mm. Most values for *U. tenuis* P.E.I. were

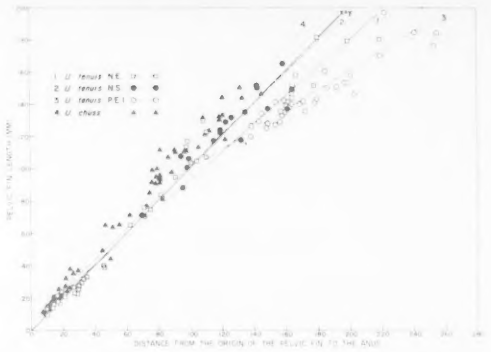

FIGURE 10.—Regression of pelvic fin length on the distance from the origin of the pelvic fin to the anus from three samples of *Urophycis tenuis* and one of *U. chuss*.

distributed above the change in slope and could not be compared to the other samples. An analysis of covariance was performed among the linear portions of the three remaining sample regressions. *U. tenuis* N.E. and *U. tenuis* N.S. were significantly different from *U. chuss* at the 1% level and from one another at the 5% level. The doubts of earlier workers concerning the validity of this character are borne out. If valid, all values for *U. chuss* would be on or to the left of the line $y = x$, and those for *U. tenuis* would be to the right of the line (Figure 10). Although most values for *U. chuss* do show this relationship, a few are to the right of the line, and many values for smaller specimens of *U. tenuis* are to the left.

Regression of Head Length on Standard Length (Figure 11, Table 1)

Regressions for all samples were linear. *U. tenuis* N.S. was not significantly different from *U. tenuis* N.E. or *U. tenuis* P.E.I. The adjusted means of the latter two were different at the 1% level. *U. chuss* was significantly different at the 1% level from all samples of *U. tenuis*. This character may be useful in distinguishing between *U. chuss* and *U. tenuis* longer than about 150 mm, particularly when used in addition to the gill raker and scale characters discussed above.

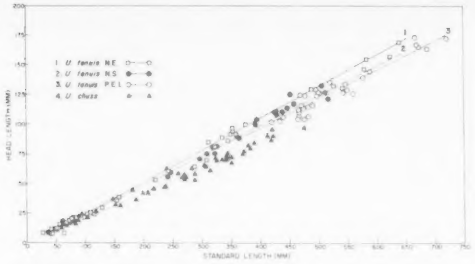

FIGURE 11.—Regression of head length on standard length from three samples of *Urophycis tenuis* and one of *U. chuss*.

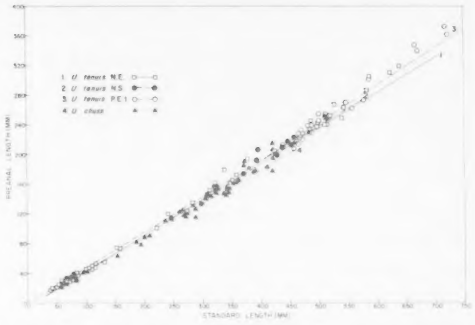

FIGURE 12.—Regression of preanal length on standard length from three samples of *Urophycis tenuis* and one of *U. chuss*.

Regression of Preanal Length on Standard Length (Figure 12, Table 1)

All regressions were linear. *U. tenuis* P.E.I. was significantly different from *U. tenuis* N.E. at the 5% level and from *U. tenuis* N.S. at the 1% level. There was no significant difference between the latter two samples. *U. chuss* was significantly different from *U. tenuis* N.E. and *U. tenuis* N.S. at the 1% level and from *U. tenuis* P.E.I. at the 5% level. Although *U. chuss* is statistically different from all samples of *U. tenuis*, there is much overlap between them and the character is not useful in species identification.

DISCUSSION

There were significant differences between *U. chuss* and all samples of *U. tenuis* for all meristic characters except the total number of vertebrae. The ranges of the numbers of lateral line scales of the two species did not overlap, and this character can be used with confidence to distinguish between them.

U. chuss invariably had three gill rakers on the epibranchial of the first gill arch, *U. tenuis* had but two. The difference is diagnostic. Mujib (1967) was in error when he reported that the epibranchial of *U. chuss* was devoid of gill rakers.

The numbers of abdominal vertebrae for each of the species showed little variability, most *U. tenuis* having 16 and most *U. chuss* having 15. This character may be valuable in identifying collections of postlarval and juvenile hakes in which the scales have not yet formed and when the mean number of abdominal vertebrae may be computed for an entire sample (Robert Marak, pers. comm.) but should not be relied upon for identification of single specimens.

None of the meristic characters showed statistically significant differences among the samples of *U. tenuis*. Such differences may exist but could have been masked by the grouping of several year classes in each sample (Appendix).

Morphometric analyses (Table 1) show that *U. tenuis* N.E. and *U. tenuis* N.S. are quite similar. *U. tenuis* P.E.I. differs from both of the latter and, of the three, is the most similar to *U. chuss*. This pattern suggests character displacement in *U. tenuis* off New England where it is sympatric with *U. chuss*. However, final judgment on the existence of character displacement should be withheld until small specimens of *U. tenuis* from the Gulf of St. Lawrence are available for examination. Morphometric differences between *U. tenuis* in the Gulf of St. Lawrence and those from Nova Scotian and New England waters may have a strong biological basis. The Gulf of St. Lawrence group gathers in large spawning aggregations during June in the Northumberland Strait (Stephen Nepszy, pers. comm.), whereas the Nova Scotia-New England group probably spawns in the fall (Musick, 1969). Thus, the two groups may be reproductively isolated.

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LITERATURE CITED

BARTLETT, M. R., AND R. L. HAEDRICH.
1966. Techniques in the radiography of fishes. Trans. Am. Fish. Soc. 95:99-101.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 576 p.

CORNISH, G. A.
1907. Notes on the Fishes of Canso. Contrib. Can. Biol. 9:81-90.
1912. Notes on fishes of Tignish, Prince Edward Island. Contrib. Can. Biol. 7:79-81.

DUNCAN, D. B.
1955. Multiple range and multiple *F* tests. Biometrics 11:1-42.
1957. Multiple range tests for correlated and heteroscedastic means. Biometrics 13:164-176.

GOODE, G. B., AND T. H. BEAN.
1895. Oceanic ichthyology. U.S. Natl. Mus., Spec. Bull. 2, 553 p.

HUBBS, C. L., AND C. HUBBS.
1953. An improved graphical analysis and comparison of series of samples. Syst. Zool. 2:49-56, 92.

HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes region. Revised ed. Cranbrook Inst. Sci., Bull. 26, 213 p.

KAUP, J. J.
1858. Uebersicht der Familie Gadidae. Arch. Naturgesch. 24(1):85-93.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

MITCHILL, S. L.
1814. Report in part, of Samuel L. Mitchill, M.D., Professor of Natural History, &c., on the fishes of New York. D. Carlisle, N.Y., 28 p. (Reprinted by T. Gill (editor), 1898, with his introduction and concordance of species.)

MOTTLEY, C. M.
1941. The covariance method of comparing the head-lengths of trout from different environments. Copeia 1941:154-159.

MUJIB, K. A.
1967. The cranial osteology of the Gadidae. J. Fish. Res. Board Can. 24:1315-1375.

MUSICK, J. A.
1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces: Gadidae). Ph.D. Thesis, Harvard Univ., Cambridge, 150 p.

RAFINESQUE-SCHMALTZ, C. S.
1818. *Phycis marginatus*, Rafinesque. New York, 27th No. 1815. *In* S. L. Mitchill, A supplement to the fishes of New York. Am. Mon. Mag. Crit. Rev., 1817-1818 2:241-248.

SNEDECOR, G. W.
1956. Statistical methods applied to experiments in agriculture and biology. 5th ed. Iowa State College Press, Ames, 534 p.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

STORER, D. H.
1839. A report on the fishes of Massachusetts. Boston J. Nat. Hist. 2:289-570.

SVETOVIDOV, A. N.
1948. Gadiformes. Akad. Nauk. SSSR, Fauna SSSR, Ryby 9(4), (Zool. Inst. N.S. 34), 221 p. (Translated by Israel Program Sci. Transl., 304 p., available Natl. Tech. Inf. Serv., Springfield, Va., as OTS 63-11071.

VLADYKOV, V. D., AND R. A. MCKENZIE.
1935. The marine fishes of Nova Scotia. Proc. N. S. Inst. Sci. 19:17-113.

APPENDIX

All specimens examined are listed in the Appendix Table. Because of the relatively large size attained by both species, it was often impossible to preserve large samples of study material in Formalin, and many fresh or frozen specimens were examined and discarded. Fresh material was collected aboard the RV *Albatross IV*, RV *Cameron*, and the trawler *Cap'n Bill III*. Also, many fresh and frozen specimens were examined from commercial catches of hake landed at Souris, Prince Edward Island.

APPENDIX TABLE—Specimens of *Urophycis chuss* and *U. tenuis* examined.

Specimen designation or catalog number	Number of specimens	Standard length (mm)	Date	Position or location		Name of vessel	Cruise number	Station number
				Lat. N	Long. W			
Urophycis chuss								
Frozen	23	237-376	27 May 1964	40°03′	69°36′	*Cap'n Bill III*		
Frozen	29	130-413	9 July 1964	3 miles S of Gay Head, Mass.		*Cap'n Bill III*		
Frozen	8	255-306	3 Aug. 1964	40°37′	67°06′	*Albatross IV*	64-10	65
Frozen	7	210-426	27 July 1964	41°09′	71°17′	*Albatross IV*	64-10	2
Frozen	11	180-470	5 Aug. 1964	41°27′	68°23′	*Albatross IV*	64-10	75
Frozen	4	371-478	16 Aug. 1964	43°08′	69°49′	*Albatross IV*	64-10	125
Frozen	2	298-519	10 Aug. 1964	Wilkinson's Basin, Gulf of Maine		*Albatross IV*	64-10	
Frozen	9	300-482	6 Aug. 1964	42°19′	69°45′	*Albatross IV*	64-10	86
Frozen	2	372-378	20 Aug. 1964	42°37′	66°34′	*Albatross IV*	64-10	162
Cleared and stained	14	19-31	15 Nov. 1960	37°27′	72°16′			
Cleared and stained	22	21-48	20 Aug. 1961	40°41′	70°06′	*Eugenie VIII*		
MCZ[1] 45420	1	119	27 Nov. 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45421	4	59-105	22 Dec. 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45422	1	154	4 Aug. 1964	41°29′	67°29′	*Albatross IV*	64-10	71
MCZ 45423	1	385	25 Feb. 1966	43°59′	62°49′	*Cameron*		
Cleared and stained	1	104	20 July 1966	40°59′	67°33′	*Albatross IV*	66-9	152
Cleared and stained	3	83-87	19 July 1966	40°48′	67°57′	*Albatross IV*	66-9	119
MCZ 45426	2	33-37	9 July 1965	42°23′	68°40′	*Albatross IV*	65-6	7
MCZ 45427	1	67	1 Nov. 1964	41°10′	67°31′	*Albatross IV*	64-13	72
MCZ 45428	1	54	28 Oct. 1964	50°07′	71°47′	*Albatross IV*	64-13	28
Urophycis tenuis								
New England:								
Frozen	1	269	9 July 1964	3 miles S of Gay Head, Mass.		*Cap'n Bill III*		
Frozen	2	278, 325	5 Aug. 1964	41°27′	68°23′	*Albatross IV*	64-10	75
Frozen	3	490-542	16 Aug. 1964	43°08′	69°49′	*Albatross IV*	64-10	125
Frozen	3	490-1,030	19 Aug. 1964	44°13′	67°54′	*Albatross IV*	64-10	150
Frozen	1	562	19 Aug. 1964	44°24′	67°33′	*Albatross IV*	64-10	151
Frozen	3	580-625	17 Aug. 1964	42°59′	68°01′	*Albatross IV*	64-10	136
MCZ 45412	12	81-273	5 Aug. 1964	41°45′	67°37′	*Albatross IV*	64-10	72
MCZ 45413	2	44-116	4 Aug. 1964	41°29′	67°29′	*Albatross IV*	64-10	71
Cleared and stained	3	51-65	21 July 1965	41°45′	67°37′	*Albatross IV*	65-10	
MCZ 45414	4	221-360	14 July 1965	43°31′	69°49′	*Albatross IV*	65-10	60
Cleared and stained	1	62	11 July 1965	41°45′	67°38′	*Albatross IV*	65-10	27
Cleared and stained	1	53	21 July 1965	41°45′	67°39′	*Albatross IV*	65-10	
MCZ 45187	1	1,119	12 July 1965	43°00′	67°55′	*Delaware*	65-6	42
MCZ 45414	2	54-58	25 May 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45415	3	38-85	4 June 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45416	1	78	7 July 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45417	1	55	14 June 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45418	1	154	24 July 1962	Great Harbor, Woods Hole, Mass.				
MCZ 45419	2	50, 68	17 May 1962	Great Harbor, Woods Hole, Mass.				
ROM[2] 4289	1	50	17 June 1927	St. Andrews, N.B.				
ROM 23088	1	59	25 July 1923	Shubenacadie River, N.S.				
ROM 9828	10	70-125	17 June 1936	Head of St. Mary's Bay, N.S.				
ROM 4291	1	51	29 June 1927	Birch Cove, N.B.				
ROM 12224	2	67, 72	9 July 1928	Passamaquoddy Bay, N.B.				
ROM 6600	1	85	5 Aug. 1915	St. Andrews, N.B.				

APPENDIX TABLE—Specimens of *Urophycis chuss* and *U. tenuis* examined.—*Continued.*

Specimen designation or catalog number	Number of specimens	Standard length (mm)	Date	Position or location		Name of vessel	Cruise number	Station number
				Lat. N	Long. W			
Urophycis tenuis—*Continued*								
Nova Scotian shelf:								
MCZ 45429	21	242-537	25 Feb. 1966	43°59′	62°49′	*Cameron*		
ROM 7070	4	38-50	16 June 1938	43°11′	62°08′			
ROM 7071	4	60-65	4 July 1938	Northeast Cove, Bedford Basin, Halifax, N.S.				
ROM 11495	4	71-80	16 June 1934	Halifax Harbor off Dartmouth, N.S.				
ROM 7072	2	65, 68	5 July 1938	Stevens Island, Bedford Basin, Halifax, N.S.				
Gulf of St. Lawrence:								
Fresh	38	422-725	July 1966	4 miles NW of Arisaig Point, Northumberland Strait by a Danish seiner				
Frozen	34	395-571	Aug. 1964	Northumberland Strait, from filleting house, Souris, P.E.I.				

[1] MCZ = Museum of Comparative Zoology at Harvard University, Cambridge, Mass.
[2] ROM = Royal Ontario Museum, Toronto, Ontario, Canada.

ALBACORE OCEANOGRAPHY OFF OREGON — 1970

WILLIAM G. PEARCY[1]

ABSTRACT

During July 1970, albacore boats trolling surface jigs (jig boats) had record catches in an area off the mouth of the Columbia River. The jig fishery declined suddenly in late July and was poor throughout the remainder of the summer. No obvious oceanographic changes were correlated with these drastic changes in fishing success. Favorable water temperatures extended through August, traditionally the month of highest albacore landings in Oregon.

Bait boats, which chum with live bait, had good fishing off Oregon from mid-August to October, indicating that the poor success of jig boats during this time was caused by the behavior of albacore relative to surface-trolled fishing gear. It is postulated that albacore descended into subsurface water in response to a change in availability of their preferred prey, the saury; here they were less accessible to jig boats than bait boats. Saury were common in the stomachs of albacore during periods of good jig fishing and were usually the dominant food where high albacore catches were made by our research vessel.

The first albacore catches of the season were probably from an area of warm temperature and low salinity representing Columbia River plume water. The subsequent migration to the north appeared to be along the oceanic edge of the plume. In general, high catches by boats were not within the core of the plume but in 15.5°C water, especially in areas where a horizontal thermal gradient was apparent.

During the summer season albacore (*Thunnus alalunga*) usually migrate into waters off the Oregon coast where upwelling and Columbia River water form a complex ecotone between coastal and oceanic waters (Owen, 1968; Pearcy and Mueller, 1970; Pearcy, 1971). The albacore fishery here fluctuates greatly among years as a result of variations of abundance and availability of albacore and fishing effort (Johnson, 1962).

Marked fluctuations of catches may also occur within a single summer and the 1970 albacore season off Oregon is a spectacular example of within-season changes in fishing success. The fishery got off to an early start in mid-July and jig boats reported exceptionally high catches (up to 1,400 fish/boat day) during late July. Record landings of over 4,000 tons were recorded for July. During late July and early August, however, the jig fishery virtually disappeared. Boats fishing in the region of the Columbia River, where high catches of 800-1,300 fish per boat day were reported on 30 July, averaged only 50 fish on 31 July.[2] Although jig fishing continued to be poor during the rest of the summer off Oregon, bait boats enjoyed good fishing into October.

The purpose of this paper is to describe ocean conditions and albacore catches in Oregon waters during the summer of 1970 in hopes of better understanding the small-scale spatial distribution of albacore tuna and the dramatic changes in their availability that occurred in 1970.

SOURCES AND TREATMENT OF DATA

Catch data for the 1970 albacore season off Oregon were derived from fish boat logs sent directly to us from fishermen or obtained through other agencies from fishermen. Thirty-three jig boats and two bait boats submitted usable records to us from our original dis-

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[2] Laurs, R.M. 1970. U.S. Bur. Commer. Fish., Albacore Bull. No. 70-3 and 70-4, La Jolla, Calif.

Manuscript accepted October 1972.
FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

tribution of 421 special logs to fishermen in Oregon, Washington, and California prior to the 1969 albacore season. These logs were unique in that they were designed to obtain several entries per day from fishermen so that variations of catch rate over small spatial areas could be examined. In addition, the Fish Commission of Oregon obtained 116 jig boat and 8 bait boat logs, California Department of Fish and Game made available 45 jig boat and 8 bait boat logs, and the Inter-American Tropical Tuna Commission provided 2 jig boat and 11 bait boat logs.

The catches of each type of boat were averaged for each day regardless of fishing location off Oregon. Catches of jig boats were also assigned to 10′ latitude × 10′ longitude blocks based on their reported loran positions. Generally catches could be assigned to a specific block. If a boat cruised over a large area and catches could not be assigned to specific blocks, the data were not plotted. No adjustment was made for the effect of boat size or number of lines on catches. It should be pointed out that our catch data do not necessarily represent average catches made by the fleet in an area because they are from only part of the fleet.

Sea-surface temperature was measured on remote sensing overflights using a Barnes PRT-5 infrared radiometer[3] at an altitude of 150 m or 500 ft (Pearcy and Mueller, 1970). A total of 15 flights were made from 22 July to 15 September on HU-16 aircraft either from the U.S. Air Force 304th Aerospace Rescue and Recovery Squadron, Portland, Oreg., or from the U.S. Coast Guard Station, Port Angeles, Wash.

On two RV *Cayuse* cruises, temperature was measured with bathythermographs, and temperature and salinity with a Salinity-Temperature-Depth system. Stations were usually 10 miles apart. On the 27 July-2 August cruise, water transparency was determined with a submarine photometer, and 6-ft Isaacs-Kidd midwater trawl collections were taken at 5 knots to a depth of about 100 m along the cruise track at night. Volume of water filtered was estimated from flowmeters mounted in the mouth of the trawl.

Albacore were caught from the *Cayuse* by fishing between hydro stations using standard trolling methods with a maximum of eight lines. Time and location of catches during daylight hours were recorded. All fish collected were measured in fork length; stomachs removed and preserved immediately with Formalin for subsequent examination of their contents.

CATCHES AND EFFORT

Statistics on catches and effort of jig and bait boats reporting to us are summarized in Figure 1. The 1970 Oregon jig season got off to an early and intense start. The first albacore of the season were reported on 15 July, the day that fishermen and processors reached a price agreement. Thereafter, three peaks of excellent fishing success occurred for jig boats: on 17, 22, and 28 July. Catches on these days averaged between 300 and 400 fish per boat day. The catch rate then declined drastically to about 55 fish per day between 28 and 31 July and never fully recovered during the remainder of the season, although success improved from 17-20 August.

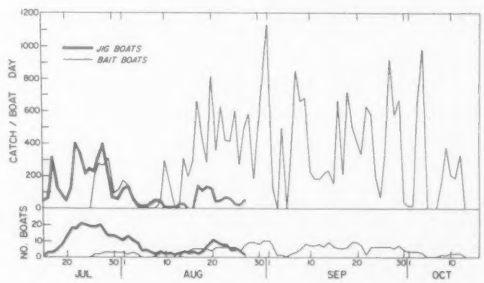

FIGURE 1.—Average number of albacore caught per day by jig boats and bait boats that submitted log sheets (above) and the number of reporting boats (below), 15 July-20 October 1970.

The number of jig boats reporting catches increased rapidly after the season began and then declined steadily from 27 July to mid-August (Figure 1). According to Laurs (see footnote 2), as jig fishing deteriorated off

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Oregon, it improved off southern California to its best level in about 3 years. For this reason the west coast jig fleet largely emigrated to California waters in August after the early collapse of the Oregon fishery.

Similar trends in the catches by both bait and jig boats existed between mid-July and early August. Peaks in catches occurred on 26-29 July and 1-2 August, followed by a common decline to very low catches on 4 August (Figure 1).

In contrast to these trends early in the season, bait boats often had excellent fishing after July, while jig fishing was poor or nonexistent. Average daily catches of bait boats remained below 320 fish per day until mid-August, followed by catches that often exceeded 500 fish per boat day from mid-August to early October. The large daily fluctuations in the catches are due in part to the small number of boats reporting.

Statistics for landings of albacore in 1970, provided by Hreha (unpublished data, Fish Commission of Oregon), are shown in Table 1. Jig boat landings were largest in July, the month of highest catches as shown in Figure 1, and progressively declined during subsequent months. According to Hreha (unpublished) about one-half of the albacore landed in August were caught in July by jig boats, and about one-half the total catch of both jig and bait boats for the 1970 season was actually caught in July. This seasonal distribution of Oregon landings in 1970 is unusual compared with other years. August is commonly the month when most albacore are landed in Oregon. Since 1961, August ranked first during 7 years and September ranked first during 2 years. July, the best month in 1970, had not ranked first in landing during the preceding 20 years (Ayers and Meehan, 1963; Meehan and Hreha, 1969).

TABLE 1.—Oregon albacore landings (metric tons and number) (Hreha, pers. comm.)

Month	Jig boat landings		Bait boat landings	
	Tons	*Number*	*Tons*	*Number*
July	3,342	450	0	0
August	2,760	869	492	13
September	569	89	2,038	55
October	306	59	130	6
Total	[1]7,218	[1]1,515	2,660	74

[1] Totals for jig boats include minor landings for November and December.

Table 1 also reveals the importance of the large jig fleet in the Oregon albacore fishing. Total landings by jig boats exceeded those by bait boats despite the deterioration of the fishing after July and despite the larger tonnage per landing (Table 1) or average catch per day (Figure 1) by the larger, but less numerous, bait boats.

MOVEMENT OF THE FLEET

Figure 2 shows the approximate location of albacore jig boats that reported catches during the summer of 1970. Generally boats were highly aggregated on a geographic basis—

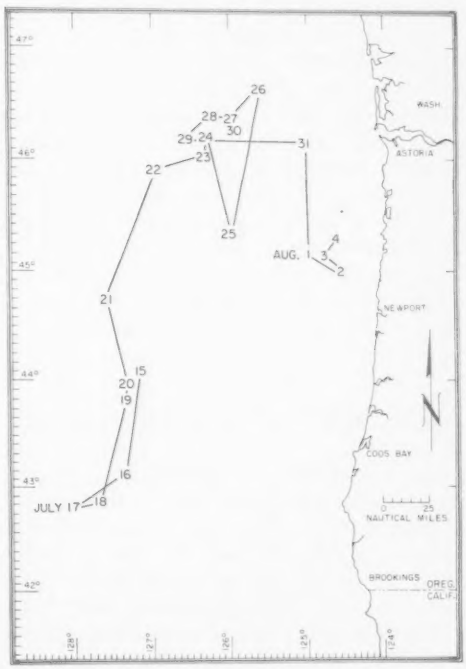

FIGURE 2.—Approximate geographic center of the albacore jig fleet from 15 July to 4 August 1970.

this plot thus estimates the central location of the fleet.

The first albacore of the 1970 season off Oregon were caught between Newport and Coos Bay on 15 July, and the subsequent early fishery during 15-21 July was localized about 140 miles off the central and southern Oregon coast. Boats shifted rapidly northward during 20-22 July and then were localized about 100 miles off the Columbia River during 22-29 July. (An exception was 25 July, when most boats moved south about 50-60 miles.) Between 29 and 31 July, during the major decline of the fishery, boats moved inshore to within 60 miles of the mouth of the Columbia River. This was followed by a shift to the south in early August and then an additional inshore movement to within 30 miles off the central coast. After 4 August the number of jig boats reporting catches was less than 11 and positions are not noted in Figure 2.

Thus the jig fishery off Oregon moved northward during July and became localized in the region off the Columbia River, where most of the fish were caught during the 1970 season. During the rapid decline of catches, jig boats moved inshore and to the south. Fishermen say that such an inshore movement of albacore may occur late in the season (September-October) when fish apparently form dense schools closer to shore and are often difficult to catch on trolled jigs. The bait boat fishery for albacore usually peaks late in the season, after jig catches decline (R. M. Laurs, pers. comm.). Thus both the inshore movement of the jig fishery and the good bait fishery occurred anomalously early in 1970.

OCEANOGRAPHIC CONDITIONS

In hopes of learning more about oceanographic conditions off Oregon and how changes in catches are related to upwelling and the Columbia River plume, we conducted weekly aircraft flights to obtain data on sea-surface temperature using infrared radiometers and fielded several cruises to determine ocean conditions both before the albacore season and later in the area of the albacore fleet. This section summarizes ocean features found during the 1970 albacore season. North-south and east-west components of winds are given in Figure 3 to aid in interpretation of wind-driven ocean circulation.

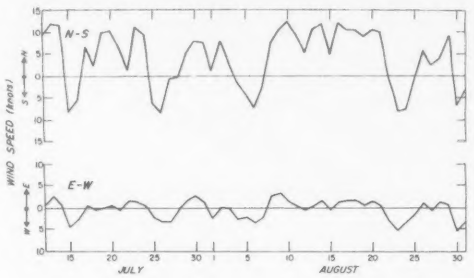

FIGURE 3.—Components of average daily wind velocities recorded at Newport, Oreg.

Cruise—7-10 July

Results of this preseason albacore cruise, off northern and central Oregon (Figure 4), illustrate the influence of both upwelling and

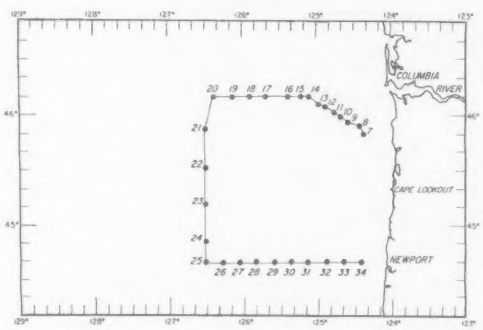

FIGURE 4.—Location of STD (Salinity-Temperature-Depth probe) stations during the preseason albacore cruise, 7-10 July 1970. (*Cayuse* 7007A).

Columbia River plume on the ocean environment. Isolines of salinity and temperature in the east-west sections (off the Columbia River and Newport, Figure 5a, b, e, f) slope upwards towards shore and are indicative of upwelling, the replacement of near-surface waters with deeper, saline, low-temperature water. The low-salinity waters of the Columbia River plume are evident in all sections. Plume

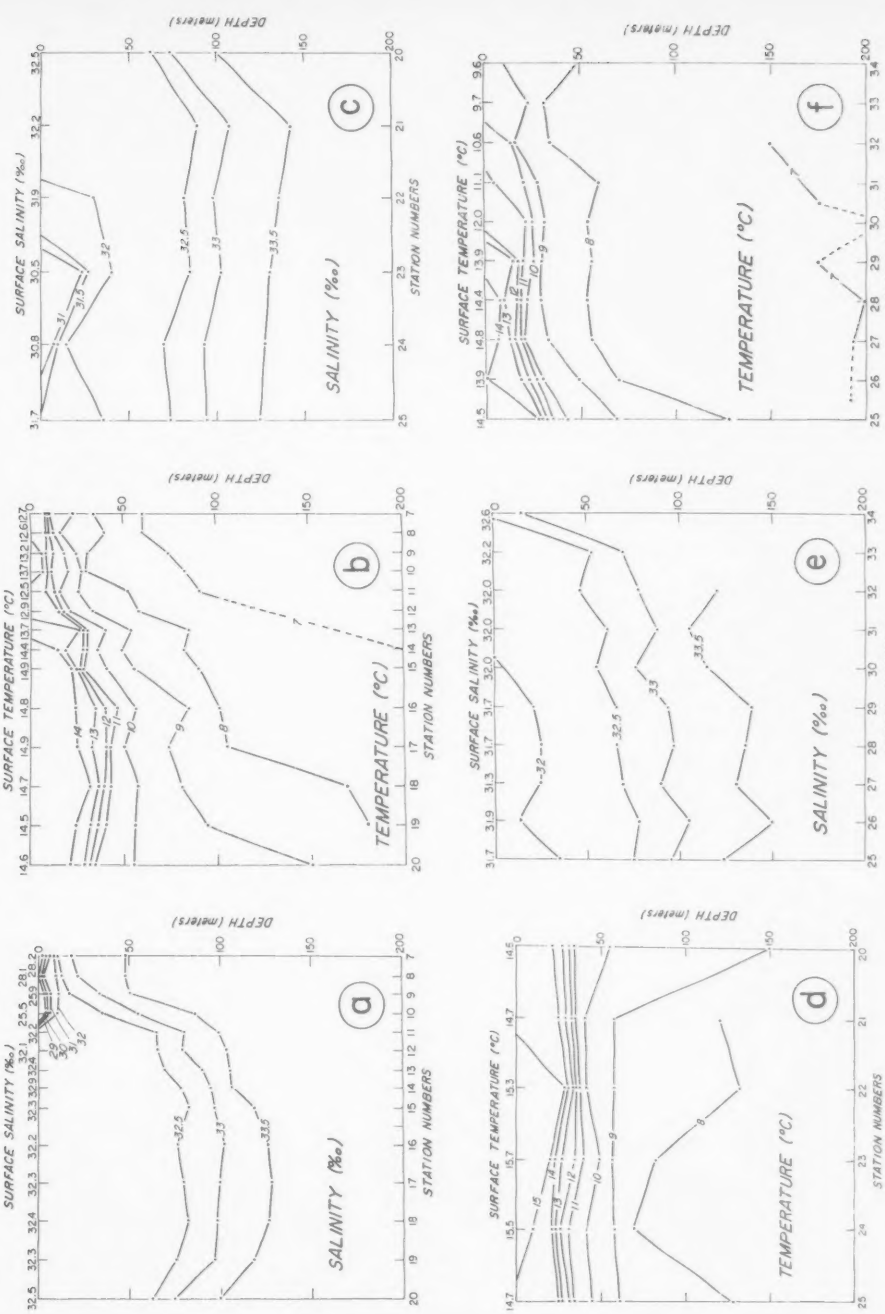

FIGURE 5.—Salinity sections: a) Stations 7-20, west of the Columbia River; c) Stations 20-25, along the north-south station line; e) Stations 25-34, along the Newport Station line. Temperature sections: b) Stations 7-20, d) Stations 20-25, f) Stations 25-34.

waters with salinities less than 32.2‰ (Owen, 1968) were found within 30 miles of shore near the mouth of the Columbia River (Stations 7-10, Figure 5a), as a lens of low-salinity water located along the north-south section 110 miles offshore (between Stations 22 and 25, Figure 5c), and greater than 50 miles offshore along the Newport transect (Stations 25-30, Figure 5e). The warmest water encountered on the cruise was along the north-south section, 110 miles offshore, where water 15°C and warmer was localized in a lens to a maximum depth of 20 m and surface temperatures as warm as 15.7°C were recorded (Figure 5d). This water, which was warmer than average in July, coincided with the low-salinity lens from the Columbia River plume. The correlation between low salinity and warm temperature early in the summer has been previously observed by Owen (1968) who described a causal basis. The strong pycnocline produced by the low-salinity water constrains mixing, and near-surface waters are heated by insolation more rapidly than surrounding waters. This relationship between salinity and temperature depends on heating rates and varies with season. Evans (1972) found that highest temperatures in the plume occurred inshore of the salinity minimum and that heat content was not a good indicator of the plume even though the temperature pattern is.

Infrared SST—15 July (Figure 6)

Our first sea-surface temperature (SST) flight was made by coincidence on the day that albacore catches were first reported off Oregon. Fish were caught about 120-160 miles off Heceta Head (Figures 2 and 6) where the fishing vessel *Spirit* reported surface temperatures of 16°C. This warm water was probably associated with a lens of low-salinity Columbia River plume water, similar to the situation found earlier in July on the cruise (Figure 5). As a result, the early location of the fishery and its subsequent movement to the north (Figure 2) may have been along plume waters, which are often the warmest waters available off Oregon during the early summer (Owen, 1968).

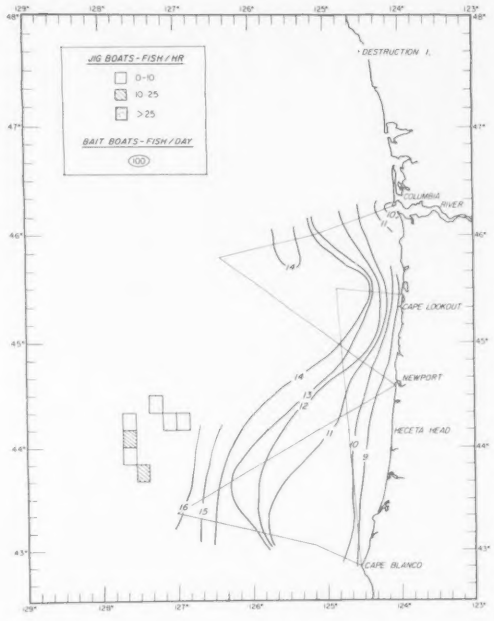

FIGURE 6.—Sea-surface temperatures (degrees Celsius) recorded by infrared radiometry on 15 July 1970. The flight track of the aircraft is shown by the narrow lines. Catch rates of albacore are indicated for jig boats by shading of 10′ blocks. In other figures, dashed lines denote isotherms based on temperatures recorded by fish boats. Daily catches of bait boats are shown by encircled numbers.

Coastal upwelling was obvious on this flight as a long band of cold (8°-9°C) water along most of the coast (Figure 6). Although average winds on 15 July were not from the direction to induce upwelling, winds on the preceding days were northerlies (Figure 3) and hence conducive to coastal upwelling. Mixture of these upwelled cold waters with the warmer Columbia River water probably masked the inshore portion of the Columbia River plume which often contrasts with upwelled water as a tongue of warm water emanating from river mouth in early summer (Budinger, Coachman, and Barnes, 1964; Owen, 1968; Pearcy and Mueller, 1970).

Infrared SST—22 July (Figure 7)

This was the day of the first large peak in average jig boat catches. (Figure 1). Most of the catches were made northwest of the SST flight and were arranged in a northeast-southwest pattern, possibly along the seaward boundary of the Columbia River plume. Highest catch rates (25-55 fish/hr) in this area were reported by fishermen trolling along the 15.5°C isotherm. High catches were also made along the 15.5°C isotherm 55 miles off Cape Lookout and along the 15°C isotherm 70 miles off the southern Washington coast.

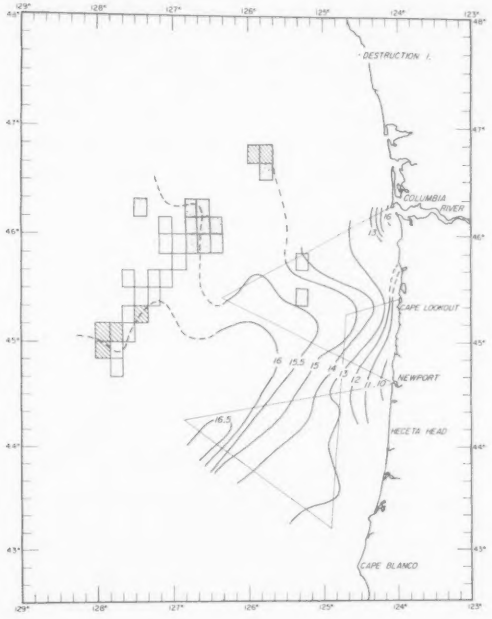

FIGURE 7.—Sea-surface temperature and albacore catch rates, 22 July 1970. Dashed lines are isotherms based on temperatures reported by fishing boats. See Figure 6 for explanation of catch notation.

The surface temperatures show an inshore-offshore gradient produced by upwelling and plume waters. Temperatures were generally warmer than on 15 July (Figure 6), however, suggesting less intense upwelling or more heating of surface waters on 22 July than on 15 July. The plume is apparent as a tongue of warm water (maximum 16.8°C) extending towards the mouth of the Columbia River.

Infrared SST—29 July (Figure 8)

This SST pattern for the day after the second big peak in jig catches (Figure 1) reflects obvious changes compared to previous patterns. Temperatures are much warmer—over 13°-14°C nearshore and over 18°C within 25 miles of the coast. These high temperatures are explained by the absence of northerly winds to induce upwelling during 26-28 July (Figure 3) and by the rapid heating of surface waters during this period of reduced wind-induced mixing, especially in the low-salinity plume that has been shifted close inshore.

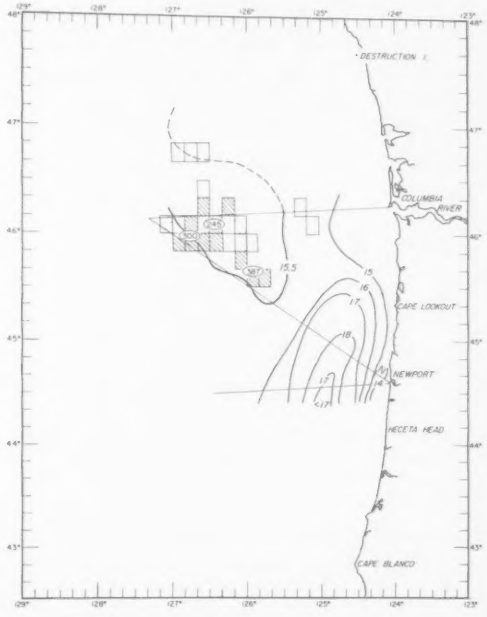

FIGURE 8.—Sea-surface temperatures and albacore catch rates, 29 July 1970. Dashed line is an isotherm based on temperatures reported by fishing boats. See Figure 6 for explanation of catch notation.

Fishing activity was localized almost entirely in a tongue of 15.5°C, blue-green water off the Columbia River (Pearcy, 1971). All the high catch rates during this day were reported

along the southern edge of this tongue. Note that three bait boats were also fishing this same region. They reported scores of 245-387 fish per day, not much higher than the jig boats which averaged 215 per day on 29 July, and below the 400 fish averaged by jig boats on 28 July.

Infrared SST—30 July (Figure 9)

The results of this SST flight show how rapidly the surface conditions can change in an area in 1 day. As a result of the onset of northerly winds (see Figure 3), renewed upwelling is now apparent along the coast between Cape Lookout and Newport. Surface temperatures near Newport were less than 10°C compared with 14°C on 29 July. Moreover, offshore temperatures were cooler on the 30th than the 29th, and no 18°C water was found on 30 July. The cooler surface water probably resulted from mixing due to increased wind stress. Note also the two separate areas of 16°C water along the southern flight lines.

Most of the fishing activity this day was again located off the Columbia River. Catches continued to decline, however, from an average of 215 fish per boat on the 29th to only 65 fish per boat on the 30th. Best success on this day (up to 17 fish/hr) was in the vicinity of 15.5°C, blue water off the Columbia River.

Infrared SST—31 July (Figure 10)

Fishing success continued its decline on 31 July with no jig boats reporting catches over 10 per hr and daily catches averaging a meager 55 albacore. Two bait boats also reported low catches, 75 and 68 fish per day.

Winds were again northerly (Figure 3) and infrared coverage by the aircraft was interrupted inshore because of the fog along the coast produced by cold, upwelled water. A pool of cool (15°C), green water was found 65 miles offshore about the same distance offshore that the band of cooler water was located on 30 July (Figure 9).

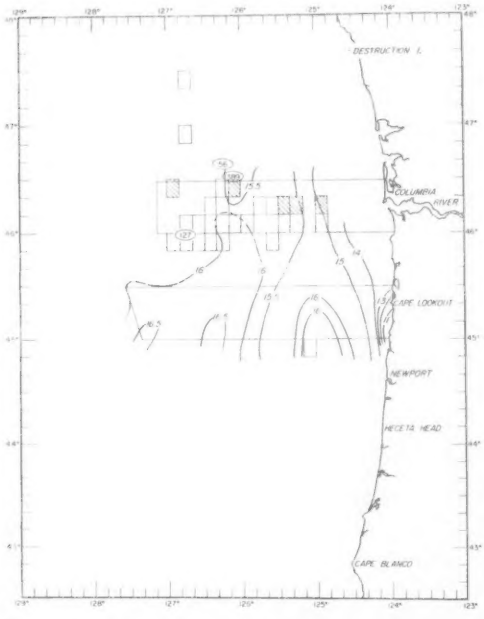

FIGURE 9.—Sea-surface temperatures and albacore catch rates, 30 July 1970. See Figure 6 for explanation of catch notation.

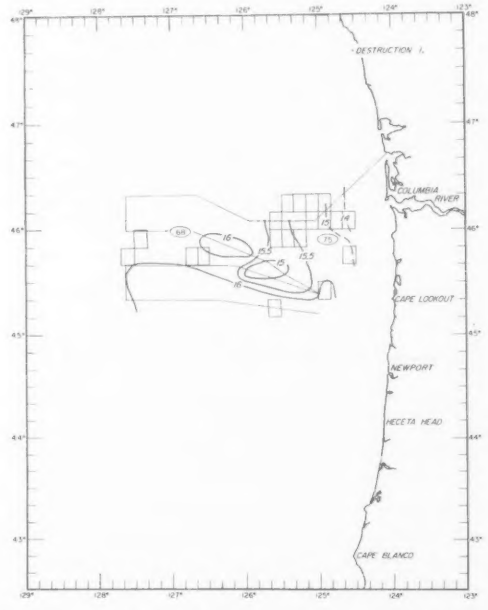

FIGURE 10.—Sea-surface temperatures and albacore catch rates, 31 July 1970. See Figure 6 for explanation of catch notation.

Infrared SST—5 August (Figure 11)

By this time the average catch of jig boats was less than 50 per day and only eight boats were reporting. The continued decline of the jig fishery did not appear to be associated with drastic changes of sea-surface temperature conditions, however. Water of 15°-16°C, was widespread offshore and south of the Columbia River.

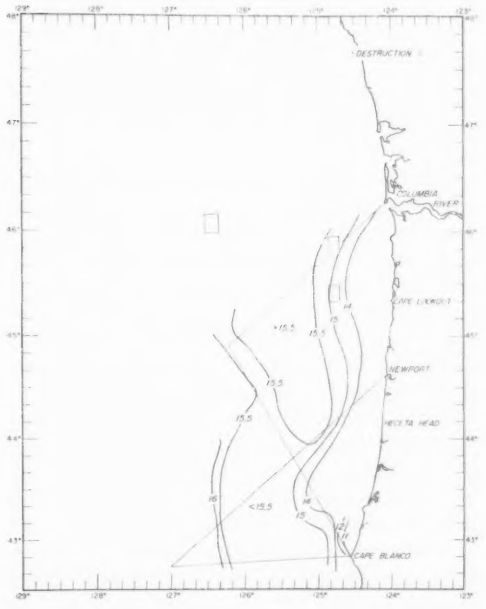

FIGURE 11.—Sea-surface temperatures and albacore catch rates, 5 August 1970. See Figure 6 for explanation of catch notation.

Coastal upwelling was not pronounced and cold water was absent inshore at Newport and the Columbia River. This situation is explained by south-westerly winds during the last 3 days (Figure 3). Plume waters were not obvious as a warmwater tongue off Oregon because of the general heating of offshore waters this late in the summer and possibly because of the lack of northerly winds that push the plume to the south along the Oregon coast.

Infrared SST—19 August (Figure 12)

During the period of 17-19 August jig catches increased to over 100 fish per day. These improved catches resulted in an increase in reported effort (10 boats on 20 August). Again sea-surface temperatures were similar to days in July when good catches were made by jig boats.

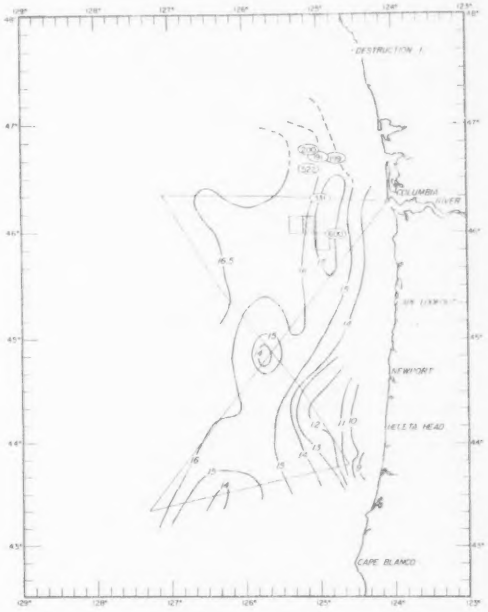

FIGURE 12.—Sea-surface temperatures and albacore catch rates, 19 August 1970. See Figure 6 for explanation of catch notation.

The six bait boats, reporting 191 to 600 fish per day, were located 30-40 miles from shore, near the mouth of the Columbia River in 15°-16.5°C water. This is the same general area where the jig boats were fishing.

Infrared SST—16 September (Figure 13)

Although no jig boats reported catches after late August, bait boats had good fishing throughout September and early October (Figure 1).

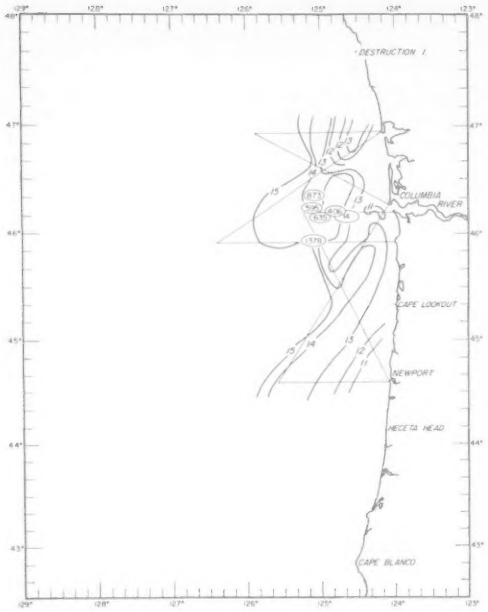

FIGURE 13.—Sea-surface temperatures and albacore catches, 16 September 1970. Numbers encircled indicate the daily catch of individual bait boats.

On 16 September bait boats were again concentrated near the mouth of the Columbia River where a finger of 14°C water extended toward shore. Judging from our data, this distribution of bait boats near the Columbia River was a common pattern, indicating favorable conditions for concentration of albacore in this area.

Cruise—27 July-2 August

A cruise was conducted in the general area of the early albacore fishery to compare oceanographic conditions in areas of high and low catch rates and to obtain albacore for a study of their food habits. The ship operated in the region of the jig fishery during the major decline in fishing success, 27 July to 2 August (Figure 1).

Oceanographic Conditions

Sea-surface temperatures measured during the week of the cruise show two regions of warm (16°C or greater) water separated by a tongue of cooler 15°-15.5°C water (Figure 14). This pattern corroborates that found on 30 July by infrared radiometry from an aircraft (Figure 9), when 16°C water was also located in two areas off the northern coast. The temperature section along the outbound cruise track extending offshore in a northwesterly direction (Depoe Bay stations) shows these two areas of warm (16°C) surface water (Figure 15). The slope of the isotherms towards the coast is indicative of upwelling, but nearshore surface temperatures were above 13°C, implying little upwelling during this period of weak winds (Figure 3). The thermocline was located between 20 and 50 m, generally deepening farther offshore.

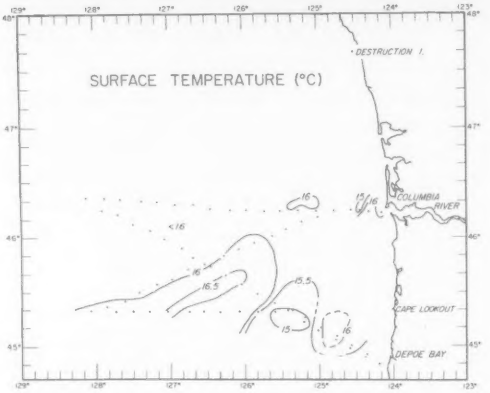

FIGURE 14.—Sea-surface temperatures recorded on the 27 July-2 August cruise. Dots indicate stations. (*Cayuse* 7007D)

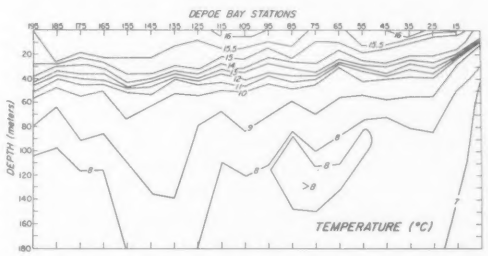

FIGURE 15.—Temperature section along the stations extending northwest of Depoe Bay on the outbound leg, 27-29 July.

The temperature section from the inbound track off Cape Lookout and Depoe Bay (Figure 16), made during the end of the cruise when

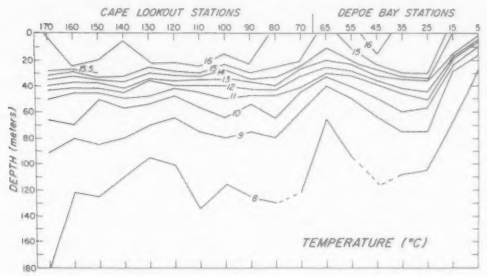

FIGURE 16.—Temperature section along the east-west stations offshore of Cape Lookout and Depoe Bay stations, inbound leg, 1 and 2 August. The Depoe Bay stations are the same ones shown in Figure 15 but 6 days later.

winds were blowing from the north, shows more evidence for upwelling than the earlier outbound track. The 15°C isotherm intersected the surface farther offshore and isotherms slope more steeply nearshore. However, surface temperatures are again not suggestive of strong upwelling. Inshore along the Depoe Bay Stations, the 16° and 15°C isotherms were deeper on the inbound than outbound legs, indicating a deepening of the mixed layer depth during the intervening time, but neither mixed layer depths beyond 75 miles off the coast or the depth of the 15°C isotherm increased noticeably with time. Surface water of 16°C was still located in two areas, which is consistent with the outbound leg, and facilitated the areal plot of surface temperature from all data.

Two extensions of low-salinity water ($<32‰$) are seen emanating from the Columbia River, one to the south and one to the southwest of the river mouth (Figure 17). These lobes of low salinity correspond with the regions of warmest temperature seen in Figure 14 and support the premise that warm water is often associated with low salinity. This correlation is not apparent close to the river mouth, however, because of admixture of plume with cool upwelled water and insufficient time for warming of the low-salinity lens.

Light extinction coefficients, calculated from photometer casts during daytime were lowest

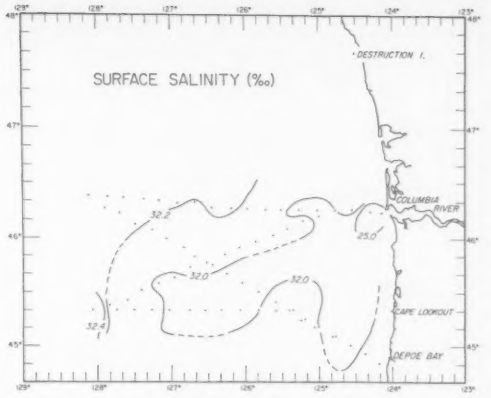

FIGURE 17.—Surface salinity measured during the cruise, 27 July-2 August 1970. Dots indicate stations.

offshore, increased in the region of the plume, and were highest along the coast (Figure 18). This agrees with Pak, Beardsley, and Park (1970) who found higher concentrations of light scattering particles in the low-salinity, warm plume waters than offshore.

Albacore Catches

The catch rates of albacore by the *Cayuse* during the cruise are shown between daylight stations in Figure 19. Highest catches were

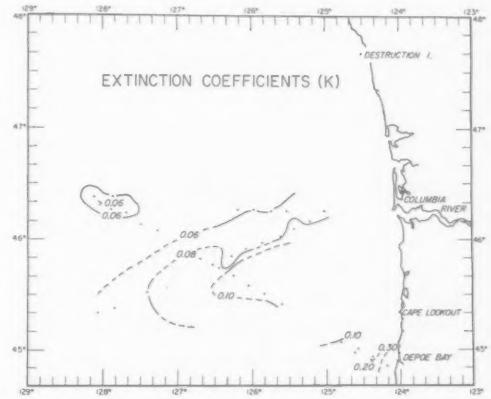

FIGURE 18.—Extinction coefficients of downwelling irradiance, $k = (\ln I_0 - \ln I_d)/d$, where I_0 is surface intensity and I_d is the intensity at depth d. Dots indicate stations where photometer casts were made.

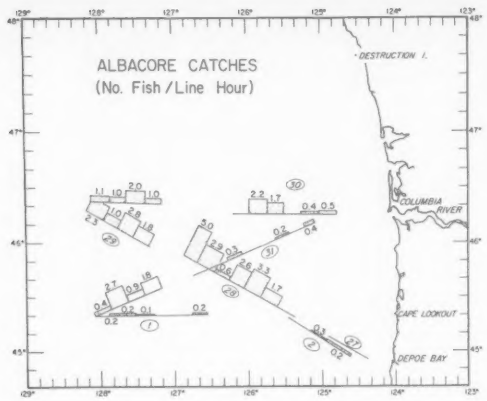

FIGURE 19.—Catch rates of albacore (fish landed per line hour) while the *Cayuse* steamed during daylight hours. Numbers above histograms indicate catch per line hour. Numbers encircled below a group of histograms denote the calendar day during the cruise (27-2 August).

made on the first half of the cruise, which corresponds to the trend of catches by commercial boats in the area (Figure 1). Fish ranged from 57 to 80 cm fork length. Catches were made along much of the cruise track and were not confined to one local area. Within individual days, however, highest catches often occurred along the offshore edge of the plume. For example, on 28 July peak catches of 3.3 and 2.9-5.0 fish/line hr were made in the vicinity of 32.0‰ and 16°C surface water (Figures 14 and 17). These were areas along the edge of the plume where the horizontal temperature and salinity gradients were more intense than in other areas (Depoe Bay Stations 85-95 and 115-135 (Figure 15)). Lowest catches on 28 July of 0.6 fish/line hr were made within the core of the plume at Stations 105-115 where salinity was 31.5‰ or lower and temperatures were above 16°C. Catches also declined along the northernmost cruise track as the ship entered a finger of 16°C and 32‰ water on 30 July.

On 31 July, after the major drop in average catches by the fleet, largest catches (2.7 fish/line hr) were not in the general area of previous high catches on 28 July but farther offshore, 160 miles off Cape Lookout. In this area the 16°C isotherm sloped to the surface (Figure 16), again indicating a horizontal thermal gradient.

A few fish were caught on 1 and 2 August, in nearshore waters, 25-50 miles off Depoe Bay. No fish were caught in the same area 6 days earlier. During the intervening time, the mixed layer depth deepened and transparency increased at the stations where fish were caught. At the station 25 miles offshore, for example, the extinction coefficient was 0.17 on 27 July compared with 0.11 on 2 August; the depth of the 15°C isotherm descended from 5 to 30 m. Thus nearshore catches late in the cruise may be correlated with increased water clarity and increased depth of favorable water temperatures.

Albacore Food Habits

The proportion of fishes, crustaceans, and squids found in the stomachs of albacore caught from the *Cayuse* is illustrated in Figure 20. In general, albacore caught within 130 miles of shore had been feeding largely on fishes, whereas squids and sometimes euphausiids were more important constituents of stomach contents farther offshore. An "S" within the pie diagrams denotes where saury, *Cololabis saira*, was the predominant food (>50% of the wet weight biomass).

On 28 July when large catches were made by the *Cayuse* and the commercial fleet, albacore were observed jumping at the surface in pursuit of saury. On this day sauries constituted nearly all the stomach contents of albacore, many of which had full stomachs. Saury predominated only twice in stomachs of albacore examined from offshore (beyond long 127°W), on 29 July and 1 August, but composed most of the stomach contents of albacore examined off the Columbia River on 30 July. Thus saury was the main forage of albacore along the outside edge of the Columbia River plume, but usually not beyond the plume during 28-30 July. After 30 July, saury was a less important food item, and ragfish, *Icosteus aenigmaticus*, and rockfish, *Sebastes*, were more common than they were earlier. In addition, sergestid shrimp constituted all the stomach contents of two albacore caught near

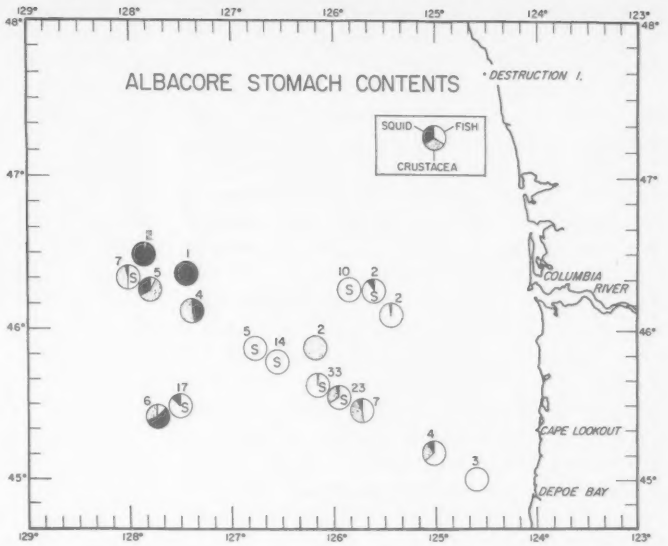

FIGURE 20.—The proportion of squids, fishes, and crustaceans (on a weight basis) in the stomach contents of albacore caught by the *Cayuse*, 27 July-2 August 1970. Numbers indicate the number of stomachs examined. "S" denotes where saury made up over 50% of the biomass of stomach contents.

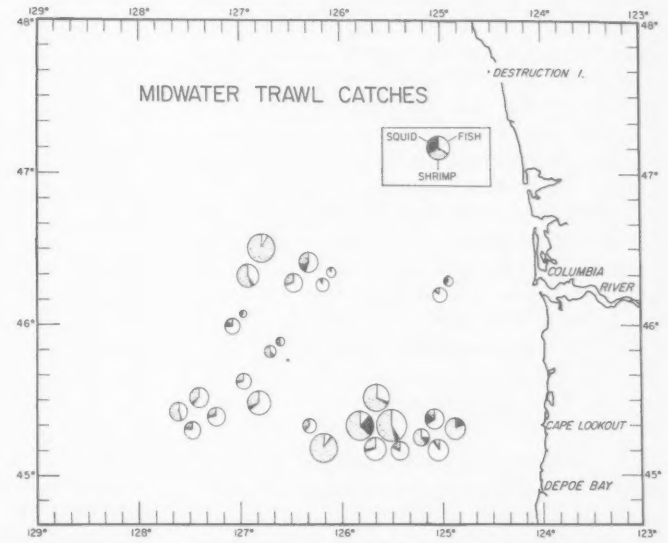

FIGURE 21.—The proportion of squids, fishes, and shrimps (on a weight basis) in 6-ft Isaacs-Kidd midwater trawl tows to 100-m depth at night, 27 July-2 August 1970. The total biomass of these groups combined for each tow is proportional to the logarithm of the diameter of the circles.

the area where saury had been eaten several days before.

Highest albacore catch rates also occurred where albacore were feeding on saury. All catch rates were ranked from highest to lowest for locations where food data was available (see Figures 19 and 20). The sum of the ranks was then compared for areas where saury predominated (>50% of the stomach biomass) and where saury did not predominate stomach contents. Catch rates were significantly higher in areas where sauries predominated stomach contents than in areas where saury were not predominant. (Mann-Whitney U Test, $P<0.01$, n_1 9, n_2 9). The decreased albacore catch rate after 28 July

is thus associated with a decreased availability of saury in near-surface waters where jig fishing for albacore is most effective.

The biomass of fishes, shrimps and squids per 1,000 m^3 of water filtered in nighttime midwater trawl tows is shown in Figure 21. Note that the diameter of the circles is proportional to the logarithm of total biomass of the tows. The highest catches were usually composed of the shrimp *Sergestes similis* in plume waters. Fishes often predominated catches, but when they did, the total biomass was generally intermediate or low. Squids were usually present but composed a relatively small portion of the biomass.

A comparison of midwater trawl catches and tuna stomach contents reveals some obvious differences. Saury was rarely if ever caught in trawls but was common as forage especially during the first part of the cruise. Squids sometimes predominated in albacore caught offshore but were unimportant components in the trawl collections, though no trawl was towed in the offshore region where squids were common in stomachs on 30 July. Few midwater trawl and albacore catch stations coincided exactly. Nevertheless the correlation between albacore catches and midwater trawl catches sometimes appeared negative. For example, lowest biomass of micronekton (Figure 21) and euphausiids (not shown) occurred in the region of high albacore catch rates (5.0 and 2.9 in Figure 19). Perhaps such a negative relationship was caused by the grazing of albacore or their carnivorous prey.

DISCUSSION

Our present state of knowledge about the behavior of albacore and the influence of the ocean environment is inadequate to explain the drastic fluctuations of catches by jig boats that occurred off Oregon in 1970. The large concentration of albacore located by the jig fleet in July 1970 off the Columbia River was very vulnerable to surface jigs and record catches were made. In contrast, boats that trolled through this same area, and Oregon waters that had been productive in past years, often reported "no fish days" in August.

Oceanographic changes that correlate with these catch variations were not obvious. Winds were variable during the entire summer with the prevailing northwesterlies being interrupted occasionally by weak frontal systems and concomittant southerly winds (Figure 3). The first large peak in catches per day was during a period of strong northerlies; the second peak, during calm sea conditions. Sea-surface temperatures remained within the "preferred" thermal range, 14.4°-16.1°C (Alverson, 1961), over much of the region during August, usually the best month for albacore fishing. Mixed layer depths also did not change appreciably and 15°C water was usually found to 20-40 m offshore of coastal waters.

The fact that bait boats had good fishing after the demise of the jig fishery suggests that albacore were present off Oregon but not susceptible to capture by jig fishing from August through mid-October. This can be explained by changes in the vertical distribution and behavior of albacore. Surface-towed jigs are most effective on fish feeding near the surface, whereas bait boats, by chumming an area, are better able to attract fish from subsurface schools.

Because albacore was feeding mainly on surface schools of saury during the second peak in jig boat success and because a significant positive relationship existed between albacore catches and feeding on saury, it is postulated that the collapse of the jig fishery was related to a change in the availability of the saury, the major prey of the albacore during the preceding period in 1970, and usually the most important food of albacore off Oregon in other years (Pearcy, unpubl. data). Saury could have been grazed down, emigrated out of the area, or descended into deeper water. Any of these could have induced the large concentration of albacore to migrate into deeper water where better feeding conditions existed and where they would be relatively inaccessible to surface trolled jigs.

During late August we repeated a cruise in the same region as the 27 July-2 August cruise, off northern Oregon and the mouth of the Columbia River. Nineteen albacore were caught on jigs. Anchovy larvae, small rock-

fishes, and *Sergestes* were the most common organisms in their stomachs. Only one saury was identified. Examination of the feeding habits of bait-caught albacore during the late summer would be of particular interest. Absence of saury from these fish would suggest that saury was not available to albacore for the remainder of the season in this region off Oregon, and albacore fed on alternate food organisms from subsurface waters. These changes in the behavior of albacore show similarities with the schooling and foraging behavior of bluefin tuna, *Thunnus thynnus*, schools off Baja California noted by Scott and Flittner (1972). They found that the occurrence of jumping and boiling schools on the surface was related to foraging on baitfish, whereas subsurface schools, which produced the largest purse seine catches per set, fed more on red crab, *Pleuroncodes planipes*.

A major conclusion of this paper is in accord with the hypothesis that the geographic range of tuna is established by temperature but food supply is largely responsible for distributions within this range (Blackburn, 1964; 1969 Nakamura, 1969). If this hypothesis is correct, it follows that accurate predictions of albacore concentrations in time and space must consider abundance and availability of forage organisms. Moreover, the depth distribution of the preferred albacore food will have pronounced influence on the relative successes of jig and bait fisheries, as the 1970 season off Oregon demonstrated.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALVERSON, D. L.
1961. Ocean temperatures and their relation to albacore tuna (*Thunnus germo*) distribution in waters off the coast of Oregon, Washington and British Columbia. J. Fish. Res. Board Can. 18:1145-1152.

AYERS, R. J., AND J. M. MEEHAN.
1963. Catch locality, fishing effort, and length frequency data for albacore tuna landed in Oregon, 1951-60. Oreg. Fish. Comm., Invest. Rep. 2, 180 p.

BLACKBURN, M.
1964. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol. Annu. Rev. 3:299-322.
1969. Conditions related to upwelling which determine distribution of tropical tunas off western Baja California. U.S. Fish. Wildl. Serv., Fish. Bull. 68:147-176.

BUDINGER, T. F., L. K. COACHMAN, AND C. A. BARNES.
1964. Columbia River effluent in the Northeast Pacific Ocean, 1961, 1962: selected aspects of physical oceanography. Univ. Wash., Dep. Oceanogr., Tech. Rep. 99, M63-18, 78 p.

EVANS, R. H.
1972. Physical parameters as tracers of Columbia River water. M.S. Thesis, Oregon State Univ., Corvallis, 55 p.

JOHNSON, J. H.
1962. Sea temperatures and availability of albacore off the coasts of Oregon and Washington. Trans. Am. Fish. Soc. 91:269-274.

MEEHAN, J. M., AND L. H. HREHA.
1969. Oregon albacore tuna fishery statistics, 1961-67. Oreg. Fish. Comm., Data Rep. Ser. 1., 143 p.

NAKAMURA, H.
1969. Tuna distribution and migration. Fishing News (Books) Ltd., Lond., 76 p.

OWEN, R. W., JR.
1968. Oceanographic conditions in the Northeast Pacific Ocean and their relation to the albacore fishery. U.S. Fish Wildl. Serv., Fish. Bull. 66:503-526.

PAK, H., G. F. BEARDSLEY, JR., AND P. K. PARK.
1970. The Columbia River as a source of marine light-scattering particles. J. Geophys. Res. 75: 4570-4578.

PEARCY, W. G.
1971. Remote sensing and the pelagic fisheries environment off Oregon. Proceedings of Symposium on Remote Sensing in Marine Biology and Fisheries Resources, Tex. A & M Univ., p. 158-171.

PEARCY, W. G., AND J. L. MUELLER.
1970. Upwelling, Columbia River plume and albacore tuna. Sixth International Symposium on Remote Sensing of the Environment, p. 1101-1113. Univ. Mich., Ann Arbor.

SCOTT, J. M., AND G. A. FLITTNER.
1972. Behavior of bluefin tuna schools in the eastern North Pacific as inferred from fishermen's logbooks, 1960-67. Fish. Bull., U.S. 70:915-927.

AGE AND GROWTH OF THE WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, ON GEORGES BANK

FRED E. LUX[1]

ABSTRACT

Lengths calculated at each scale annulus from 510 winter flounder, *Pseudopleuronectes americanus*, collected on Georges Bank during 1963-66 provided a measure of growth up to 12 years of age. Growth was more rapid on Georges Bank than on inshore areas. Females grew faster than males after age 2. Fish from eastern Georges Bank grew slightly faster than those from western Georges Bank. Bertalanffy growth equations were computed for each sex.

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), found in Atlantic coastal waters from Newfoundland to Cape Hatteras, is a common fish in the New England and middle Atlantic catch. Landings by commercial fishermen, mostly with otter trawls, averaged 12,000 metric tons annually in the period 1966-70. In addition, there is a large sport fishery since the species occurs in shallow coastal waters easily accessible to saltwater anglers. The estimated angler catch in 1965 was 13,000 tons (Deuel and Clark, 1968).

Most of the catch is made in the New England area where the species is found on both inshore and offshore grounds. There appear to be a number of distinct groups in this area, judging from movement of tagged fish and variation in numbers of fin rays (Perlmutter, 1947; Bigelow and Schroeder, 1953; Lux, Peterson, and Hutton, 1970). One of these groups is on Georges Bank where the fish are larger and have more fin rays than on inshore areas. There is almost no movement of winter flounder between Georges Bank and inshore grounds. The growth material presented here is for winter flounder from Georges Bank.

On the basis of size, color, and fin ray number, Kendall (1912) determined that the winter flounder from Georges Bank comprised a separate species, which he named *P. dignabilis*. Bigelow and Schroeder (1953), however, considered the differences as no more than racial, a view which presently prevails.

Studies of winter flounder growth on inshore areas, summarized by Berry, Saila, and Horton (1965), Poole (1966), and Kennedy and Steele (1971) indicated that age determination from hard body parts is difficult and that growth rate varied with area. Females grew faster than males, at least after the first few years.

There is no previous study on growth of winter flounder on Georges Bank although it has long been known that winter flounder there grow much larger than on inshore grounds (Bigelow and Schroeder, 1953).

MATERIALS AND METHODS

The fish for the study were obtained from research vessel and commercial catches in 1963-66. The research vessel samples were from National Marine Fisheries Service *Albatross IV* groundfish surveys (Grosslein, 1969). Since the otter trawl used had a ½-inch mesh liner in the cod end, both large and small fish were obtained. Six additional samples were collected from catches of commercial otter trawlers, and these contained only fish greater than 36 cm in total length.

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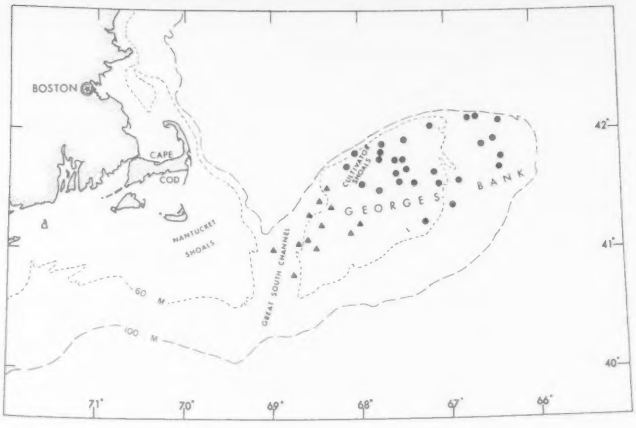

FIGURE 1.—Locations on Georges Bank where winter flounder were collected for age and growth studies. (Dots: eastern Georges Bank; triangles: western Georges Bank.)

Locations where samples were taken for the study cover most of the northern half of Georges Bank (Figure 1). Otter trawl catches from the *Albatross IV* groundfish surveys suggest that there are two somewhat separate areas of winter flounder abundance on Georges Bank. The area of greatest abundance extends from Cultivator Shoal eastward to about long 67°W. This is the area where most of the Georges Bank commercial catch is taken. The other area is southwest of Cultivator Shoal and extends westward from there to about long 69°W. The two areas are roughly shown by plotting catches of winter flounder from eight groundfish surveys on Georges Bank (Figure 2). Although sampling was relatively uniform over the entire Bank to a depth of 200 m (see figures in Grosslein, 1969), catches of five or more winter flounder per otter trawl station were made only in the above-defined areas. Growth was computed separately for fish from these two areas (Figure 2).

Scales were used for age determination since these appeared easier to interpret than otoliths and had the advantage of greater ease for calculation of lengths at earlier ages. The scales were removed from the eyed side of fish along the lateral line in the area just anterior to the caudal peduncle. Total length in millimeters and sex were recorded for each scale sample. Except where noted, lengths given herein are total lengths.

Impressions of the scales were made in transparent cellulose acetate strips. These were viewed with a microprojector using 40× magnification, and year marks (annuli) were identified and counted. Criteria for distinguishing annuli were the same as those used for New England yellowtail flounder, *Limanda ferruginea*, (Lux and Nichy, 1969) which, like the winter flounder, have ctenoid scales. With the exception of the first year, spring and summer growth was characterized by widely spaced circuli (rapid length accretion) and fall and winter growth, by closely spaced circuli (slow length accretion). The outer edge of the zone of closely spaced circuli was con-

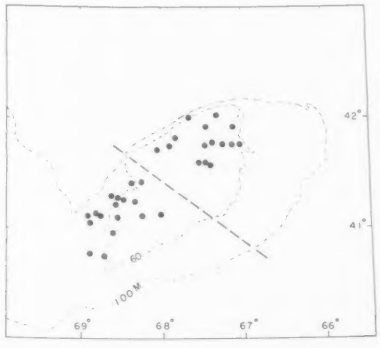

FIGURE 2.—Georges Bank stations (30-min otter trawl hauls) where five or more winter flounder were caught during fall groundfish surveys in 1963-70. (Dashed line indicates the boundary between east and west Georges Bank for the growth study.)

sidered to be the annulus. Slight checks in growth consisting of only a few closely spaced circuli were considered to be false annuli and were ignored in assigning age. In the first year all circuli are closely spaced. The annulus here was taken to be the outermost of these circuli.

Ages were assigned to each fish by the author and, independently, by an assistant. For some scales reliable growth calculation appeared impossible because of regeneration, erosion, resorption, or checks. These, making up about 15% of the total sample, were omitted from the calculations. As might be expected, the proportion of rejected scales was much higher for large fish (Table 1).

TABLE 1.—Length-frequency distribution of winter flounder collected on Georges Bank in 1963-66 and proportions included in the growth calculations, by 5-cm intervals.

Length interval (cm)	Total number of fish	Included in calculations	
		Number	Percent
11-15	4	4	100.0
16-20	11	11	100.0
21-25	18	18	100.0
26-30	27	26	96.3
31-35	28	28	100.0
36-40	80	73	91.2
41-45	108	101	93.5
46-50	158	133	84.2
51-55	94	69	73.4
56-60	55	38	69.1
61-65	15	8	53.3
66-70	4	1	25.0
Total	602	510	84.7

Age was determined, to the extent possible, for the rejected scales and length at age of these fish was compared with that of fish included in the growth calculations to determine if bias was introduced by the rejection of part of the sample (Figure 3). While the samples were rather small in the older ages, there appeared to be no difference in growth of the two groups of fish.

Totals of 412 fish from eastern Georges Bank and 98 from western Georges Bank were included in the calculations. All of the commercial samples, consisting of 225 fish, were from eastern Georges Bank.

Length at each annulus was calculated from measurements of anterior scale radii. The relationship of body length to scale length approximated a straight line, except for curvilinearity among the smallest fish (Figure 4). Direct proportion growth calculations therefore were made using the equation

$$l_n = C + \frac{S_n}{S}(l - C)$$

where l_n is the fish length at the time of formation of the nth annulus, C is the fish length at scale formation, S_n is the anterior scale radius to the nth annulus, S is the anterior scale radius at capture, and l is the

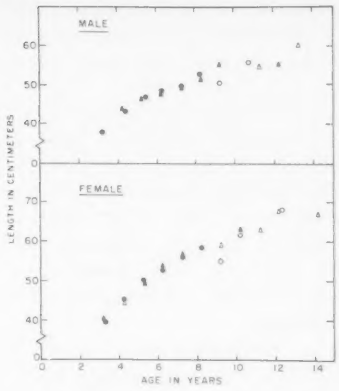

FIGURE 3.—Mean lengths at capture by age group for fish from commercial samples included in growth calculations (circles) and those rejected (triangles). (Open symbols represent fewer than three fish.)

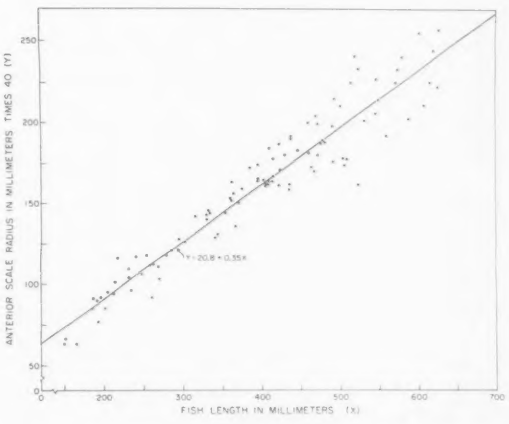

FIGURE 4.—Body-scale relationship of Georges Bank winter flounder based on measurements of 101 fish.

fish length at capture (Fraser, 1916). Two scales were measured for each fish. A nomograph was used to facilitate computations (Carlander and Smith, 1944).

For the value of C an estimated fish length at scale formation of 20 mm was used. This was based on examination of winter flounder 17 to 25 mm long collected in Massachusetts coastal waters in early June 1962 (Lux and Nichy, 1971). I have assumed that scale formation occurs at about the same length on Georges Bank where I have collected no fish of the above sizes.

Evidence, indicating that marks identified as annuli on the scales of winter flounder from Georges Bank were actual year marks, was obtained from several sources. The main lines of this evidence are summarized below.

1. There is a correlation between age and size in that increase in number of annuli is accompanied by an increase in fish size (Figure 5).
2. Lengths at various annuli calculated from scales correspond with empirical lengths at the same ages determined from reading scales (Figure 5).
3. There is agreement on length at age of fish from the same age-groups collected in different years (Table 2) and agreement on calculated growth among different year classes (Tables 3 and 4).
4. Distinguishing permanent marks consisting of unpigmented spots on the eyed side of the fish occurred in successive years in an estimated 4 to 13% of winter flounder from the 1959 year class on eastern Georges Bank (Lux, in press). This white spotting appears to occur in far less than 1% of the fish of a year class normally. White-spotted fish of the 1959 year class were collected in 1964, 1965, and 1966. Those from 1964 had 5 annuli on their scales; those from 1965, 6 annuli, and those from 1966, 7 annuli, showing that 1 annulus was added each year. The mean lengths of spotted fish from this year class showed regular increases over these 3 years (Table 5). Growth rate was unaffected by white spotting.

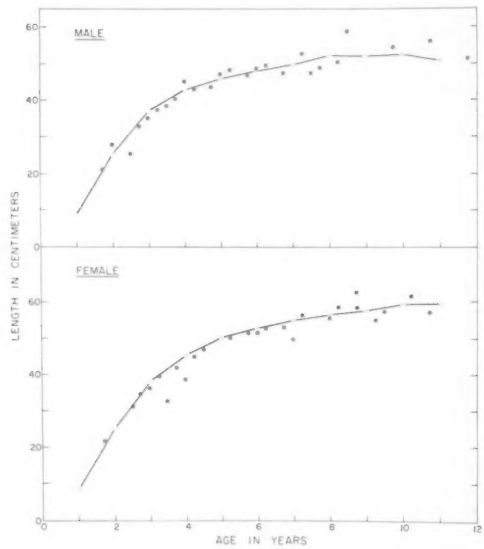

FIGURE 5.—Mean length at age from scale age determinations (dots) compared with mean calculated length at each annulus (open circles) for male and female winter flounder from eastern Georges Bank.

TABLE 2.—Number (n) of fish in each sample and mean length in centimeters (cm) at capture by age group for male and female winter flounder from eastern Georges Bank in 1963-66.

Age group	Year caught	Male		Female	
		n	cm	n	cm
II	1965	12	29.4	8	32.7
	1966	8	30.1	5	35.8
III	1964	2	38.2	4	39.4
	1965	5	38.4	3	32.7
	1966	27	39.3	38	39.2
IV	1963	—	—	1	47.8
	1964	18	43.8	18	45.0
	1965	—	—	2	46.6
	1966	11	43.4	10	42.9
V	1964	20	47.1	7	50.8
	1965	—	—	—	—
	1966	14	46.6	9	50.5
VI	1964	10	48.3	7	50.6
	1965	12	49.3	11	54.1
	1966	18	47.8	10	52.1
VII	1963	1	51.4	—	—
	1964	5	49.8	—	—
	1965	1	44.1	2	55.8
	1966	24	49.6	28	55.0
VIII	1964	6	54.3	1	61.0
	1965	1	58.9	—	—
	1966	4	51.0	7	56.6

TABLE 3.—Number (n) of fish in each sample and calculated mean length in centimeters (cm) at each annulus, for each year class and for all year classes combined, for male and female winter flounder collected on eastern Georges Bank in 1963-66.

Year class	Number of annuli																							
	1		2		3		4		5		6		7		8		9		10		11		12	
	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm
Males																								
1955	2	6.2	2	19.2	2	33.6	2	40.8	2	44.6	2	46.6	2	47.8	2	49.0	2	50.0	1	50.4	1	50.8	—	—
1956	4	11.4	8	24.4	8	38.5	8	45.1	8	49.2	8	51.2	8	52.5	7	54.0	1	54.3	1	55.1	—	—	—	—
1957	5	8.6	8	23.8	8	38.1	8	43.8	8	47.4	8	49.7	8	51.0	3	54.2	2	53.4	—	—	—	—	—	—
1958	9	7.5	15	22.6	15	36.4	15	42.5	15	45.8	15	47.8	5	48.4	4	50.7	—	—	—	—	—	—	—	—
1959	46	9.8	56	28.0	56	39.0	56	43.9	56	46.5	36	48.4	24	49.2	—	—	—	—	—	—	—	—	—	—
1960	27	8.2	36	25.8	36	37.6	36	43.2	18	45.8	18	47.5	—	—	—	—	—	—	—	—	—	—	—	—
1961	11	7.8	16	23.4	16	36.1	14	42.6	14	45.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	12	8.3	16	24.9	16	36.3	11	41.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	34	7.1	39	24.7	39	35.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964	8	8.6	8	25.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	26	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	184	8.2	204	25.5	196	37.3	150	43.3	121	46.4	87	48.4	47	49.9	16	52.6	5	52.2	2	52.7	1	50.8	—	—
Females																								
1954	1	6.2	2	23.9	2	40.0	2	49.2	2	54.4	2	57.6	2	59.9	2	61.6	2	62.7	2	63.6	1	66.8	1	67.4
1955	1	8.2	3	28.1	3	40.6	3	46.6	3	50.4	3	52.1	3	53.7	3	54.7	3	55.7	2	55.4	2	56.0	—	—
1956	1	10.5	2	22.7	2	39.6	2	46.3	2	51.4	2	54.0	2	56.3	2	57.8	1	56.6	—	—	—	—	—	—
1957	3	9.1	3	25.6	3	39.9	3	46.3	3	50.2	3	52.8	3	54.6	3	55.9	3	56.9	—	—	—	—	—	—
1958	10	6.9	16	22.0	16	37.6	16	44.6	16	48.9	16	51.6	9	54.8	7	56.2	—	—	—	—	—	—	—	—
1959	43	10.8	47	29.5	47	40.8	47	47.2	46	50.8	39	53.4	28	55.0	—	—	—	—	—	—	—	—	—	—
1960	21	8.2	28	24.0	28	37.6	28	44.7	10	49.0	10	51.6	—	—	—	—	—	—	—	—	—	—	—	—
1961	10	7.2	15	23.6	15	37.8	11	44.6	9	48.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	7	6.4	13	19.3	13	32.2	10	40.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	38	7.9	46	24.7	38	36.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964	2	8.7	5	24.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	26	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	163	8.4	180	25.1	167	38.0	122	45.4	91	50.1	75	52.8	47	55.1	17	56.7	9	57.7	4	59.5	3	59.6	1	67.4

[1] Includes males and females.

RESULTS

The computed lengths at each annulus for male and female winter flounder from eastern and western Georges Bank in 1963-66 (Tables 3 and 4, Figure 5) show that females grow faster than males after the second year. This pattern of growth is similar to that of New England yellowtail flounder in which sexual maturity usually occurs at age 3 (Lux and Nichy, 1969). Limited evidence from the present study indicates that Georges Bank winter flounder also begin to attain maturity at age 3.

The fish from western Georges Bank appeared to grow a little less rapidly, at least in early years, than those from the eastern part of the Bank, and their growth is therefore presented separately (Tables 3 and 4, Figure 6). However, the sample from western Georges Bank is too small to precisely define growth there. Growth in length for both of the grounds is rapid until age 5 or 6. Then it tends to decrease sharply, especially for males (Figure 6).

Growth by year class on eastern Georges Bank (Table 3) suggested that fish from the 1959 year class grew slightly faster than those from other years. The data at hand, however, are inadequate for a conclusive examination of this question.

Following the first 2 years, the growth of fish on Georges Bank is faster than that of fish on inshore areas (Figure 6). Although the growth of this species on the inshore grounds apparently varies widely from place to place

TABLE 4.—Number (n) of fish in each sample and calculated mean length in centimeters (cm) at each annulus for each year class and for all year classes combined, for male and female winter flounder collected on western Georges Bank in 1963-66.

Year class	Number of annuli																					
	1		2		3		4		5		6		7		8		9		10		11	
	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n	cm
Males																						
1958	3	6.3	6	17.9	6	31.2	6	39.0	6	44.3	2	49.0	2	50.8	—	—	—	—	—	—	—	—
1959	3	5.9	3	17.0	3	29.9	3	36.9	3	40.6	3	43.4	1	43.5	—	—	—	—	—	—	—	—
1960	12	6.4	14	21.1	14	34.4	5	38.8	5	42.2	4	45.4	—	—	—	—	—	—	—	—	—	—
1961	6	6.6	6	20.8	4	28.5	4	36.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1962	4	7.1	4	19.2	4	35.1	2	44.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	18	7.2	18	23.1	7	35.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	1	9.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	47	6.8	51	21.0	38	33.2	20	38.6	14	42.8	9	45.5	3	48.4	—	—	—	—	—	—	—	—
Females																						
1954	1	8.6	1	25.2	1	38.8	1	46.4	1	50.5	1	54.2	1	56.6	1	58.8	1	60.4	1	61.6	1	62.4
1955	1	8.2	1	17.2	1	27.6	1	37.2	1	45.4	1	50.0	1	54.0	1	56.4	1	58.0	1	59.0	—	—
1956	3	7.3	3	21.9	3	35.5	3	44.5	3	49.7	3	53.4	3	55.9	2	58.4	2	60.0	1	61.0	—	—
1957	2	6.2	2	17.6	2	29.0	2	38.8	2	44.6	2	48.2	2	50.9	2	52.6	—	—	—	—	—	—
1958	1	6.7	1	20.0	1	30.2	1	37.4	1	40.9	—	—	—	—	—	—	—	—	—	—	—	—
1959	5	7.7	5	24.1	5	37.1	5	44.1	5	49.8	5	52.6	1	55.6	—	—	—	—	—	—	—	—
1960	12	7.3	14	21.8	14	33.5	14	39.8	14	44.5	1	53.6	—	—	—	—	—	—	—	—	—	—
1961	9	7.4	9	19.7	7	29.6	7	37.1	1	42.4	—	—	—	—	—	—	—	—	—	—	—	—
1962	2	6.8	2	20.3	2	36.2	2	42.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1963	4	7.1	5	23.5	4	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964	1	14.0	1	26.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1965[1]	1	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	42	7.5	44	21.6	40	33.6	36	40.4	28	46.1	13	52.1	8	54.5	6	56.2	4	59.6	3	60.5	1	62.4

[1] Sex unknown.

TABLE 5.—Length-frequency distributions of white-spotted winter flounder of the 1959 year class obtained from commercial catches in 1964-66 from eastern Georges Bank.

Length (cm)	May-June 1964		April 1965		April 1966	
	Male	Female	Male	Female	Male	Female
46	3	1	1	—	—	—
47	3	—	3	—	4	—
48	2	—	—	—	2	—
49	4	—	3	—	—	—
50	1	1	3	—	5	—
51	1	—	1	1	1	—
52	—	3	—	—	2	3
53	—	2	1	3	—	—
54	—	—	1	4	—	4
55	—	—	—	1	—	3
56	—	—	—	2	1	4
57	—	—	—	1	—	3
58	—	—	—	1	—	2
59	—	—	—	—	—	3
60	—	—	—	—	—	1
Total	14	7	13	13	15	23
Mean	48.0	51.1	49.4	54.5	49.7	55.9

(Berry et al., 1965; Poole, 1966; Kennedy and Steele, 1971), it does not approach the rate on Georges Bank at any inshore location where it has been described. Growth of females was greater than males after the first few years in all areas, except off Newfoundland where there appeared to be no difference in the age range covered (Figure 6).

Calculated growth to the first annulus was about 7 or 8 cm for both sexes on Georges Bank (Tables 3 and 4). Although no 0-group fish were obtained from Georges Bank for length comparison, this size agrees closely with the lengths of 0-group winter flounder from inshore Massachusetts waters (Lux and Nichy, 1971). There the 0-group fish by late fall averaged 8.7 cm long in 1961 and 7.3 cm in 1962. There was no apparent growth difference with sex in these inshore fish, for in late October 1962 the males were 7.3 cm long (n =

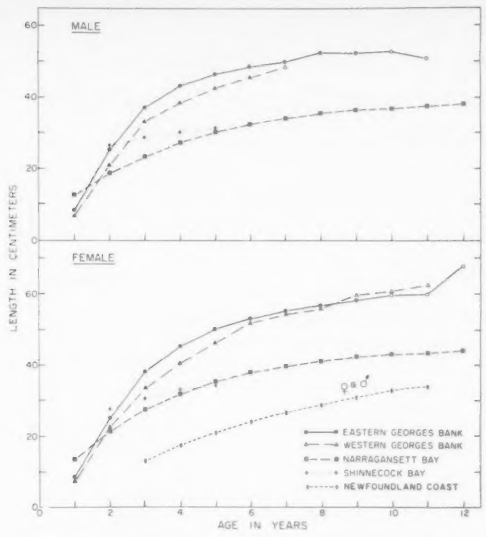

FIGURE 6.—Mean calculated lengths at each annulus for male and female winter flounder from Georges Bank compared with growth data for fish from Narragansett Bay, R.I. (Berry et al., 1965), Shinnecock Bay, N.Y. (Poole, 1966), and Conception Bay, Newfoundland (Kennedy and Steele, 1971). (Open symbols for Georges Bank represent fewer than five fish.)

10) and females, 7.2 cm (n = 18). Length in late fall of the first year in Connecticut waters in 1958 and 1959 was similar to the above, being about 7.0 cm standard length (Pearcy, 1962), which is about 8.7 cm total length. Lengths calculated at the first annulus on otoliths of winter flounder in Rhode Island waters by Berry et al. (1965) were somewhat greater, being 12.5 cm for males and 13.5 cm for females.

Bertalanffy growth equations of the form

$$l_t = l_\infty [1 - \exp(-K(t - t_0))]$$

in which l_t is length at age t, l_∞ is the theoretical maximum length, K is the rate of change in length increment, and t_0 is the age at which growth in length theoretically begins, were fitted by the method of Ricker (1958), to the mean lengths at each age for males and females from eastern Georges Bank (Table 3). The resulting equations

$$l_t = 550 [1 - \exp(-0.37(t + 0.05))] \quad \text{(male)}$$
$$l_t = 630 [1 - \exp(-0.31(t - 0.05))] \quad \text{(female)}$$

express the growth rates for fish of age 3 and beyond (Figure 7).

Estimates of l_∞ given here are principally for use in developing a mathematical expression of growth rather than to accurately portray maximum attained length. The l_∞ of 55.0 cm for males, for example, is somewhat shorter than the maximum observed length of 57.0 cm. Likewise, the l_∞ of 63.0 cm for females is considerably shorter than the 70.0 cm maximum observed.

Inclusion of more large and old fish in the samples might have altered the form of the computed growth curves slightly. Until more accurate equations are derived, however, those given above will provide reasonable accuracy for yield per recruit calculations for both eastern and western Georges Bank.

ACKNOWLEDGMENT

Robert N. Hersey, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, made independent age determinations of the fish included in this study and performed most of the growth calculations. His assistance is gratefully acknowledged.

LITERATURE CITED

BERRY, R. J., S. B. SAILA, AND D. B. HORTON.
1965. Growth studies of winter flounder, *Pseudopleuronectes americanus* (Walbaum), in Rhode Island. Trans. Am. Fish. Soc. 94:259-264.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

CARLANDER, K. D., AND L. L. SMITH JR.
1944. Some uses of nomographs in fish growth studies. Copeia 1944:157-162.

DEUEL, D. G., AND J. R. CLARK.
1968. The 1965 salt-water angling survey. U.S. Fish Wildl. Serv., Resour. Publ. 67, 51 p.

FRASER, C. M.
1916. Growth of the spring salmon. Trans. Pac. Fish. Soc. 2d Annu. Meet., p. 29-39.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

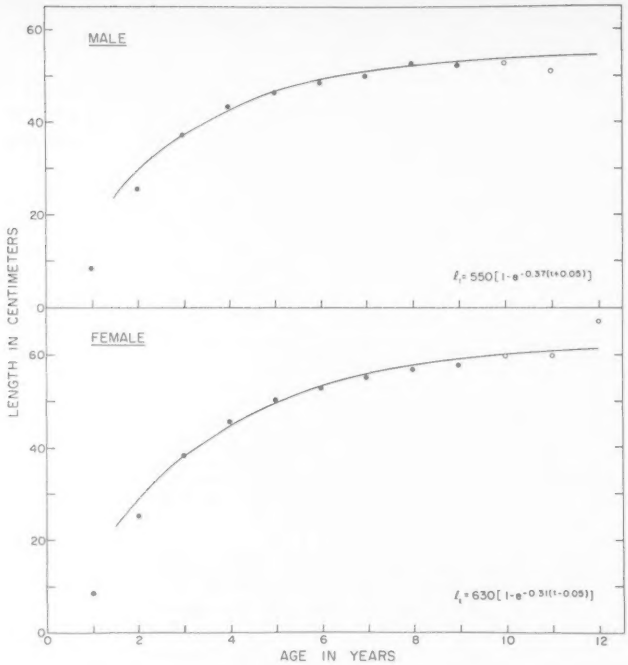

FIGURE 7.—Mean calculated lengths at each annulus for male and female winter flounder from eastern Georges Bank and the fitted Bertalanffy growth curves. (Open circles represent fewer than five fish.)

KENDALL, W. C.
1912. Notes on a new species of flatfish from off the coast of New England. Bull. U.S. Bur. Fish. 30:389-394.

KENNEDY, V. S., AND D. H. STEELE.
1971. The winter flounder (*Pseudopleuronectes americanus*) in Long Pond, Conception Bay, Newfoundland. J. Fish. Res. Board Can. 28:1153-1165.

LUX, F. E.
In press. White spotting in the 1959 year-class of Georges Bank winter flounder, *Pseudopleuronectes americanus* (Walb.). Trans. Am. Fish. Soc.

LUX, F. E., AND F. E. NICHY.
1969. Growth of yellowtail flounder, *Limanda ferruginea* (Storer), on three New England fishing grounds. Int. Comm. Northwest Atl. Fish., Res. Bull. 6:5-25.
1971. Number and lengths, by season, of fishes caught with an otter trawl near Woods Hole, Massachusetts, September 1961 to December 1962. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 622, 15 p.

LUX, F. E., A. E. PETERSON, JR., AND R. F. HUTTON.
1970. Geographical variation in fin ray number in winter flounder, *Pseudopleuronectes americanus* (Walbaum), off Massachusetts. Trans. Am. Fish. Soc. 99:483-488.

PEARCY, W. G.
1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). Bull. Bingham Oceanogr. Collect. Yale Univ. 18(1):1-78.

PERLMUTTER, A.
1947. The blackback flounder and its fishery in New England and New York. Bull. Bingham Oceanogr. Collect. Yale Univ. 11(2):1-92.

POOLE, J. C.
1966. Growth and age of winter flounder in four bays of Long Island. N.Y. Fish Game J. 13:206-220.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

PROBLEM OF BIAS IN MODELS TO APPROXIMATE OCEAN MORTALITY, MATURITY, AND ABUNDANCE SCHEDULES OF SALMON FROM KNOWN SMOLTS AND RETURNS

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ABSTRACT

The problem of methodological bias in estimating ocean mortality or survival, maturity, and abundance of multireturn species of Pacific salmon (*Oncorhynchus* spp.) is examined heuristically with a data base for which no unbiased estimators exist. The case of hatchery coho salmon (*O. kisutch*) is emphasized to treat the problem in its simplest form (two returns). Models previously reported by Ricker, Fredin, and Cleaver are considered in the context of their application in biomass computations and the particular problem of bias in approximating average and interval-specific mortality coefficients during ocean life. A new scheme is introduced as the limit-mean model, and the assumptions in all four models are contrasted. Numerical examples for a hypothetical cohort demonstrate a wide range of bias in estimates of different parameters from the same model and also in estimates of the same parameter from different models applied in different situations. For the hypothetical data, overall performance is best for the limit-mean model with the offshore catch known; this model also provides estimates of natural and fishing mortality rates offshore during the last year at sea. For coho and chinook salmon, (*O. tshawytscha*) caught off western North America, it is recommended that 1) maturity be directly sampled to help provide nominally unbiased estimates for certain of the parameters and 2) research be intensified on determining offshore catch by origin independently of marking smolts.

Three oceanic fisheries have motivated research on the geographic origins, distribution patterns, and changes in biomass during the marine life of salmon. One is the Japanese mothership fishery, since 1952 by drift gill nets west of long 175°W in the North Pacific Ocean—mainly for pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon (Fukuhara, 1953). Another is the offshore troll and sport fishery from California to Alaska for chinook (*O. tshawytscha*) and coho (*O. kitsutch*) salmon (Godfrey, 1965; Mason, 1965). Third is the drift net fishery for Atlantic salmon (*Salmo salar*), since 1964 off southeast Greenland and northern Norway (Horsted, 1971).

The results of biomass computations based on growth and natural mortality estimates must be combined with catches (real or assumed) by natal origin in order to assess the impact of offshore vis-a-vis inshore fishing (Taguchi, 1961a, 1961b; Doi, 1962; Ricker, 1962, 1964; Parker, 1963; Fredin, 1964; Hirschhorn, 1966; Cleaver, 1969; Henry, 1971, 1972). Investigators have recognized the scarcity of existing field data, the high cost of direct marking/recovery at sea, and the technical difficulties of obtaining unbiased data and constructing realistic models to approximate the time distribution of mortality (Ricker, 1962; Parker, 1960, 1962, 1963, 1968; Fredin, 1964; Lander et al., 1967; Cleaver, 1969).

Biased estimates can distort the interpretation of actual time changes in biomass of a cohort and impede the application of rational conservation measures. On the other hand, reasonably accurate approximations to interval-specific mortality can be useful not only in biomass computations: they may help also to predict returns from the sea and thereby to improve management of inshore salmon fisheries (e.g., Gilbert, 1963).

In this report I review three published models for approximating ocean mortality schedules

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as applied in biomass computations, examine the particular problem of bias in mortality estimates, and introduce another model to extend the indirect approach developed by Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969). Bias in estimated maturity and abundance schedules is examined also.

METHODS AND LIMITATIONS

The indirect approach is applicable to species in which maturing adults from the seaward migrants in a given year (or smolt class) return to their natal area in 2 or more years: single-return pink salmon are excluded. The following minimum data are required for multireturn species: 1) origin-specific number of seaward migrants or smolts in a given year, 2) number of survivors returning from the ocean each year until the smolt class is extinct, and 3) intervals between times of seaward migration and of each return or spawning escapement. An offshore fishery may or may not exist; origin-specific catch data for the inshore fishery or an offshore fishery may or may not be available. No unique solution exists for the mortality, maturity, and abundance schedules from the foregoing data base: different combinations of mortality and maturity schedules can generate the same set of observed data.

I consider only the bias due to the absence of unique solutions in estimating models. Data on the numbers of smolts and returning adults may be biased additionally in practice; in fact, the very existence of basic data is unfortunately the exception in wild stocks (e.g., Gilbert, 1963). Data as observed in practice are assumed here to be accurate in order to emphasize the methodological problem.

The number of mortality, maturity, and abundance parameters increases formidably with the number of returns and with the possible regimes of offshore-inshore exploitation. The case of only two returns, typical of hatchery and most wild stocks of coho salmon south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972), is emphasized throughout.

Finally, the study is heuristic. Explicit equations for bias are available for only two of the four models as treated here. The equation for one of the two is tedious to write for just one parameter—say the monthly coefficient of total mortality between times of outmigration and of the last return—and descriptive equations for bias are very cumbersome when estimates for all mortality, maturity, and abundance parameters are considered. Relations among all parameters are evident from initial description of the actual situation, however, and are utilized for some numerical comparisons from a set of hypothetical data. These numerical comparisons of bias are selective also with respect to the two general cases considered: 1) catch data unknown and 2) catch data known from marking (or otherwise identifying) smolts and from sampling the catch for recoveries. I try to avoid unfair comparisons between models, to compare them where justified, and to demonstrate how small bias in one parameter estimate may translate to large bias in another estimate from the same model.

ACTUAL SITUATION

Pertinent events of the life history (Shapovalov and Taft, 1954; Godfrey, 1965; Johnson, 1970; Drucker, 1972), observational data, and parameters are related below for coho salmon in the southern part of their freshwater range in North America.

Spawning occurs during November-January and typically the surviving fry are free-swimming during the next February-April. The cohort stays in fresh water until downstream migration of survivors begins about a year later at time $t = t_0$; the actual time of entry to the ocean, some weeks later, depends on physiological condition, stream flow and temperature, and distance from spawning areas. Our mortality schedule starts at time $t = t_0$ and includes downstream mortality of smolts unless their number is known when they enter the sea.

The first return from the sea is in the year of outmigration (6-9 mo later) and occurs at time $t = t_1$, usually during October-December or about 2 years after eggs are spawned. This first return is all or nearly all males or "jacks."

Few jacks are recorded from offshore fisheries but some are taken in freshwater fisheries. Time $t = t_1$ ends our first mortality interval and starts the second.

The immature age-2 fish remaining at sea (males plus females) are reduced in numbers by natural mortality alone for about 6-8 more mo until their recruitment to offshore fishing at time $t = t_r$. For about 5 mo thereafter, offshore then inshore fishing operate along with natural mortality. About a year after the jacks return, age-3 adults appear in the final escapement at time $t = T$ to render the smolt class extinct for our purposes. Thus t_1 and t_r divide the effective life span, $T - t_0$, into three subintervals.

Basic notation follows:

N_0 = number of smolts at time $t = t_0$
E_1 = number of jacks in first return or spawning escapement at time $t = t_1$
N_1 = number of age-2 immatures at sea at time $t = t_1$
N_r = number of recruits to offshore fishing at time $t = t_r$
C = number of fish caught offshore
E_2 = number of adults in second (last) return or spawning escapement at time $t = T$
m = fraction of the cohort which matures as jacks near time $t = t_1$
s_1, s_2 = survival fractions during $t_1 - t_0$ and $t - t_1$, respectively
Z_1, Z_2 = monthly coefficients of natural plus fishing mortality during $t_1 - t_0$ and $T - t_1$, respectively
M_2 = monthly coefficient of natural mortality during $T - t_1$
F = monthly coefficient of fishing mortality in offshore waters during $T - t_r$
Z_T^* = monthly coefficient of total mortality during $T - t_0$
u = exploitation rate in offshore fisheries
e = base of natural logarithms.

The following relations summarize the actual situation:

$$E_1 = N_0 s_1 m = m N_0 e^{-Z_1 (t_1 - t_0)}. \tag{1}$$

$$\begin{aligned} N_1 &= N_0 s_1 (1 - m) \\ &= (1 - m) N_0 e^{-Z_1 (t_1 - t_0)}. \end{aligned} \tag{2}$$

$$N_r = N_1 e^{-M_2 (t_r - t_1)}. \tag{3}$$

$$\begin{aligned} C &= u N_r = [F/(F + M_2)] \\ &\quad \times [1 - e^{-(F + M_2)(T - t_r)}] N_r. \end{aligned} \tag{4}$$

$$\begin{aligned} E_2 &= N_r e^{-(F + M_2)(T - t_r)} \\ &= N_1 e^{-M_2 (T - t_1) - F(T - t_r)} \\ &= N_1 s_2 = N_1 e^{-Z_2 (T - t_1)} \\ &= N_0 s_1 s_2 (1 - m) = N_0 s_1 s_2 - E_1 s_2 \\ &= (1 - m) N_0 e^{-Z_T^* (T - t_0)}. \end{aligned} \tag{5}$$

We have also the general definitions of the mortality coefficients:

$$\begin{aligned} Z_T^* &= (-\ln s_1 s_2)/(t - t_0) \\ &= [Z_1 (t_1 - t_0) + Z_2 (T - t_1)]/(T - t_0). \end{aligned} \tag{6}$$

$$\begin{aligned} Z_2 &= (-\ln s_2)/(T - t_1) \\ &= [M_2 (T - t_1) + F(t - t_r)]/(T - t_1). \end{aligned} \tag{7}$$

$$Z_1 = (-\ln s_1)/(t_1 - t_0). \tag{8}$$

If the smolts are not marked (or otherwise identified) to estimate C and the inshore catch by origin, then the escapement data (E_i) come from hatchery counts or natural spawning areas. If only the inshore catch is identified by origin, a value of E_i is the sum of inshore catch plus "escapement" from inshore fishing to the spawning area in a given year (usually called the "return" or "run" by salmon biologists); it occurs somewhat earlier in time and of course exceeds the value of E_i without inshore catch data available. Thus with inshore catch data available, $Z_1 = M_1$ (the offshore catch of jacks being absent or negligible), Z_2 includes only offshore mortality, and $Z_2 = M_2$ if no offshore fishery exists ($F = C = 0$). The indirect approach was developed mainly from data without offshore fishing mortality but with inshore catches known. If an offshore fishery exists (as on the coho salmon emphasized

here), both C and the inshore catch may be identified by origin (e.g., Worlund, Wahle, and Zimmer, 1969; Johnson, 1970). The possibilities of 1) C known but inshore catch unknown with respect to origin or 2) offshore fishing present but inshore fishing absent are too remote for consideration here. Our two general cases—C known and unknown—are therefore defined and the inshore catch is implicit in E_i. Figure 1 contrasts the extinction of a smolt class with and without offshore fishing.

It is evident from Equations 1-5 that the s_i and m are confounded, and no unique solution exists. This fact and the existence of offshore salmon fisheries led to development of the indirect approach.

ESTIMATING MODELS

Three existing models are reviewed in terms of biomass computations, bias in estimated mortality schedules is considered, and a new estimating scheme is introduced.

Ricker's (1962) Model

This model is based on convincing if indirect evidence (not direct measurements) that most natural mortality during the ocean life of sockeye salmon occurs well before the fish are large enough to be recruited to an offshore fishery. In the context of Equations 6-8 with $F = C = 0$:

$$[M_1(t_1 - t_0) + M_2(t_r - t_1)]/(t_r - t_0) = M_r^* > M_2. \quad (9)$$

In Equation 9, M_r^* is the average monthly rate of natural mortality during $t_r - t_0$, t_0 being the date when (say) half the smolt class enters the sea in 1 year and t_r the date of potential recruitment offshore the next year (say). Parker (1968) demonstrated from direct marking/recovery of pink salmon that natural mortality is highest during the first few weeks of ocean life. To my knowledge, salmon biologists all agree that $M_1 > M_2$.

In the absence of direct measurements, Ricker's model assumes $m = 0$ and $s_2 = 1.0$ on the E_1 jacks (Equations 1 and 5); it treats $E_1 + E_2 = \Sigma E_i$ as a single escapement at time $t = T$, with the following result from Equation 5:

$$\hat{Z}_T^* = \hat{Z}_i = \hat{M}_i = M_{rL}^* = M_{2U} = -\ln(\Sigma E_i/N_0)/(T - t_0). \quad (10)$$

In Equation 10 the caret symbol ($\hat{}$) denotes an estimate, and the subscripts L and U denote lower and upper limits, respectively.

Because $M_{2U} < \hat{G}$ (the estimated growth coefficient) after $t = t_r$ for most age and maturity groups of commercial size in offshore waters, Ricker (1962) concluded that offshore fishing is biologically wasteful. Those biomass computations assume 100% availability to an offshore fishery, however, and overestimate minimum losses. Ricker (1964) later mentions the availability in connection with the growth-mortality balance in pink and chum salmon and computes weight losses from offshore fishing as a fraction of maximum possible yield (inshore fishing only) for any fixed spawning escapement required for reproduction. Biomass calculations of Parker (1963) and Fredin (1964) also assume full availability. Although the evidence indicates offshore fishing reduces total yield (see also Cleaver, 1969; Henry, 1971, 1972), I emphasize that schedules of growth, mortality, and availability must be combined in order to assess the impact of existing or potential offshore fisheries: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock offshore.

Ricker's model (Equation 10) was applied only to situations where $F = C = 0$. The direction if not the magnitude of bias in the mortality schedule is known from evidence already cited, i.e., $\hat{M}_1 < M_1$ and $\hat{M}_2 > M_2$. When an offshore fishery exists ($F > 0$ in Equation 4) and $Z_1 = M_1$ as noted for coho salmon, Equation 10 may be used as the estimator, $\hat{Z}_T^* = \hat{Z}_1 = \hat{Z}_2$, and the bias defined in terms of known data and the unknown maturity parameter, m. Absolute bias (B) is defined as:

$$B = \text{estimate minus parameter value.} \quad (11)$$

Applying Equations 10 and 11 and the actual values of Z_i from Equations 1 and 5 when C is unknown:

$$B_{(\hat{Z}_T^*)} = [T - t_0]^{-1}[-\ln(\Sigma E_i/N_0) + \ln(E_2/N_0) - \ln(1-m)]. \quad (12)$$

$$B_{(\hat{Z}_1)} = [T - t_0]^{-1}[-\ln(\Sigma E_i/N_0)] + [t_1 - t_0]^{-1}[\ln(E_1/N_0 - \ln m]. \quad (13)$$

$$B_{(\hat{Z}_2)} = [T - t_0]^{-1}[-\ln(E_i/N_0)] + [T - t_1][\ln(E_1/N_0) - \ln(E_2/N_0) - \ln m + \ln(1-m)]. \quad (14)$$

Fredin's (1964) Model

Ricker's model accounts for the magnitude but not for the actual timing of preultimate returns (again, for the magnitude of E_1 in Equations 1-5 here). Fredin (1964) accounts both for magnitude and actual timing. His Model 1 is based on Equation 11 of Parker (1962), who separates relatively high natural mortality on small juveniles plus returning adults—both in inshore waters—from relatively low natural mortality in offshore waters. Parker's results actually derive, however, from his Equations 13 and 14 and utilize data from paired groups of marked smolts. I consider only the information available from a single group of smolts (marked or unmarked).

Thus Model 1 of Fredin (1964) assumes with Ricker (1962) that $Z_T^* = Z_1 = Z_2$; more strictly, the assumption is again that $M_T^* = M_1 = M_2$ because Fredin deals also with data not influenced by offshore fishing. Substituting the assumption in Equation 5 gives an estimator in the relation:

$$E_2/N_0 = e^{-\hat{Z}_T^*(T - t_0)} - (E_1/N_0)e^{-\hat{Z}_T^*(T - t_1)}. \quad (15)$$

Equation 15 is solved by trial and error unless one applies more advanced mathematical properties. Equation 15 differs from Equation 10, so values of $\hat{Z}_T^*$ from the same data obviously will differ. We anticipate less bias in $\hat{Z}_T^*$ from Equation 15 because it accounts for the actual timing of the E_1 jacks. With no explicit definition for $\hat{Z}_T^*$ in Equation 15, however, relations for bias (e.g., Equations 12-14) cannot be written and Equation 15 is later evaluated numerically.

Finally, Fredin's Models 2-4 employ various assumptions to accord with the reality, $Z_1 > Z_2$ (or $M_1 > M_2$). Although no "estimators" in the sense of Equation 15 are available from his Models 2-4 in the indirect approach, it is interesting that calculated maturity schedules were relatively insensitive to the different time distributions of mortality Fredin assumed between his Models 1-4.

Cleaver's (1969) Model

This model was developed specifically to utilize inshore and offshore catch data as known from a landmark study which evaluated the bioeconomic contribution of 1961-64 brood chinook salmon from Columbia River hatcheries (Worlund et al., 1969). Its basic assumption in the context of Equations 1-5 is that $M_2 = 0$ during $T - t_1$. The result is one-sided limits for certain parameters:

$$E_2/(C + E_2) = s_{2U} = e^{-Z_{2L}(t - t_1)}. \quad (16)$$

$$N_{1L} = E_2/s_{2U} = C + E_2. \quad (17)$$

$$m_U = E_1/(E_1 + N_{1L}). \quad (18)$$

As actually applied (Cleaver, 1969; Henry, 1971), the model used data on four escapements to the river (E_i) at ages 2-5 from a given smolt class and data on offshore catches (C_i) of immature plus currently maturing fish at ages 3-5 (unfortunately, marked recoveries in the offshore catch were not sampled for maturity—the catch being taken by small vessels and landed dressed with heads on). Values of E_i and C_i led to rejection of the hypothesis that Z_i was constant for ages 3-5 in offshore waters (certain resulting values of $m_i > 1.0$ implying more mature fish than were present in the total marked populations). Rejection of constant Z_i was deduced (by values of C_i and E_i) to be mainly from variation in F_i. Recalling the basic assumption ($M_i = 0$ during the last year or $M_2 = 0$ here), the authors then examined

the effects on M_i, F_i, and N_i of constant, nontrivial values of natural mortality, M_C, on all recruited age groups ($M_2 > 0$ during $T - t_r$ in our notation). The effect of offshore fishing on hatchery stocks in terms of age-specific escapements to the river was computed (with $F = 0$) for different values of M_C.

The model yields no point estimators and therefore no equations for bias, but is important here for several reasons. First, it utilizes known offshore catch data for the first time in the indirect approach. Second, it emphasizes the need for direct sampling of the offshore catch for maturity by origin (i.e., after marking smolts): the resulting $\hat{m}$ would give nominally unbiased estimates of all parameters but F and M_2 in Equations 1-8. Third, the calculated maturity schedules changed little with changes in M_C after recruitment to offshore fishing (Cleaver, 1969; Henry, 1971); this agreement with Fredin's (1964) result, based on varying the time distribution of natural mortality during all of ocean life for sockeye salmon, evidently is quite general for the 3-4 returns these three authors treated. Finally, reliance of the Cleaver model on one-sided limits (Equations 15-17) led directly to development of the last model.

Limit-Mean Model

Given the foregoing development of the indirect approach, it is natural to consider 1) devising two-sided limits on (say) Z_i or s_i initially and 2) taking for each parameter a value intermediate between these limits as a nontrivial estimator with unknown bias. The opposite and usual procedure in population problems is to derive nominally unbiased estimators and their variances (thus confidence limits) from statistical theory (e.g., the change-in-ratio estimators reported definitively by Paulik and Robson, 1969).

Offshore Catch Unknown

In this case C may be considered "unknown" because either 1) no offshore fishery exists ($Z_i = M_i$) on the target population and we deal actually with the M_i as Ricker (1962) and Fredin (1964) did, or 2) an offshore fishery exists (Z_2 includes $F > 0$ as in our coho salmon) but techniques to evaluate $C > 0$ are not applied. The survival product, $s_1 s_2$, is the target parameter. Limits on the s_i are devised initially with the help of Assumption 1 ($s_{1U} = s_{2L} = s$) and Assumption 2 ($s_{2U} < 1.0$).

Assumption 1 is based on the evidence cited earlier which demonstrates almost incontrovertibly that $M_1 > M_2$. Now $t_1 - t_0$ (Equation 1) is shorter for coho salmon emphasized here—6-9 mo at the outside—than the $T - t_1 \simeq 12$ mo of ocean life remaining in the stocks south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972). It is most unlikely that $s_1 > s_2$, however, even when the intensive offshore fishery during $T - t_r \simeq 4$-5 mo is considered. Assumption 1 gives from Equation 5 the quadratic:

$$s^2 - (E_1/N_0)s - E_2/N_0 = 0 = s_{1U} s_{2L} = (s_1 s_2)_L . \quad (19)$$

Only one root is possible and the solution of Equation 19 is:

$$s = s_{1U} = s_{2L} = 0.5 \left\{E_1/N_0 + [(E_1/N_0)^2 + 4E_2/N_0]^{1/2}\right\} . \quad (20)$$

A reasonable value for Assumption 2 ($s_{2U} < 1.0$) depends on the stock and species. Murphy's (1952) often cited point estimates for coho salmon during their last year of ocean life serve as a guide for later numerical illustration. His estimates are 16-51% for 12 successive smolt classes (1938-49); only three estimates exceed 50%, of which two are 51%. Today's more intensive offshore fishery probably reduces s_2 below that in 1947 to which his estimated maximum, $\hat{s}_2 = 57\%$, applied. [In the next section I use $s_{2U} = 50\%$ but assign no value here. Other estimates and limits warrant mention: 68% by Parker (1962) as a point value grossly averaged for various smolt classes, stocks, and species; 51-80% as point estimates for sockeye salmon by Fredin (1965) and Mathews (1968); and 39-73% as upper limits by Cleaver (1969) for chinook salmon of ages 3-5 taken along with coho salmon

offshore.] Applying Assumption 2 in Equation 5:

$$(E_2 + E_1 s_{2U})/N_0 = s_{1L} s_{2U} = (s_1 s_2)_U. \quad (21)$$

The geometric mean of limits in Equations 19 and 21 is then taken arbitrarily to be the estimator:

$$\begin{aligned}[(s_1 s_2)_L (s_1 s_2)_U]^{1/2} &= [\{0.25E_1/N_0 + [0.25(E_1/N_0)^2 + E_2/N_0]^{1/2}\} \\ &\quad \times (E_2 + E_1 s_{2U})/N_0]^{1/2} \\ &= \hat{s_1 s_2} = e^{-\hat{Z}_T^*(T - t_0)}. \end{aligned} \quad (22)$$

From Equations 1-3, 5, and 22 we finally have:

$$\begin{aligned}\hat{s}_2 &= (\hat{s_1 s_2} - E_2/N_0)/(E_1/N_0) \\ &= e^{-\hat{Z}_2(T - t_1)}. \end{aligned} \quad (23)$$

$$\hat{s}_1 = \hat{s_1 s_2}/\hat{s}_2 = e^{-\hat{Z}_1(t_1 - t_0)}. \quad (24)$$

$$\hat{N}_1 = E_2/\hat{s}_2. \quad (25)$$

$$\hat{m} = [1 - E_2/E_1 \hat{s}_2]^{-1} = E_1/(E_1 + \hat{N}_1). \quad (26)$$

$$\hat{N}_r = \hat{N}_1 e^{-\hat{Z}_2(t_r - t_1)}. \quad (27)$$

The form of the middle member of Equation 26 (from the ratio of Equation 5 to Equation 1) is included for its practical import: if an offshore catch is identified by origin from any technique whatsoever, then subsampling it for maturity gives an independent estimate ($\hat{m}$) from which s_2 then can be estimated without data on the number of smolts. As noted in connection with Cleaver's model, an independent maturity estimate also gives nominally unbiased estimators for the system when N_0 is known (excluding, again, the subdivision of $\hat{Z}_2$ into $\hat{F}$ and $\hat{M}_2$ as evident from Equation 7 when $t_r \neq t_1$). Even though all estimates contain unknown bias, with no offshore fishery the values of $\hat{Z}_2$ ($=\hat{M}_{2U}$) from Equation 23 and of $\hat{N}_r$ from Equation 27 might prove useful in biomass computations.

Offshore Catch Known

It is not necessary to assume as in the Cleaver model that $M_2 = 0$ during all of $T - t_1$. Assumption 3 is: $M_2 = 0$ during $T - t_r$ when offshore fishing occurs. This gives:

$$N_{rL} = C + E_2. \quad (28)$$

Solving Equation 20 (as in the case of C known) and inserting the result in Equation 2:

$$N_{1U} = N_0 s_{1U} + E_1. \quad (29)$$

Assumption 4 is: $F = 0$ during $T - t_r$. By Assumptions 3 and 4 we would observe $C + E_2$ instead of just E_2 at time $t = T$ (similarly, Ricker's model utilizes $E_1 + E_2$ at time $t = T$). Because $C + E_2$ and N_{1U} are both too high, the coefficient, X, relating these artificial population sizes may be defined and used as below:

$$X = -\ln[(C + E_2)/N_{1U}]/(T - t_1). \quad (30)$$

$$N_{rU} = N_{1U} e^{-X(t_r - t_1)}. \quad (31)$$

The geometric mean of limits in Equations 28 and 31 is taken arbitrarily as the estimator:

$$(N_{rL} N_{rU})^{1/2} = \hat{N}_r. \quad (32)$$

We then have from Equations 4 and 5, 7, and 32:

$$C/\hat{N}_r = \hat{u}. \quad (33)$$

$$-\ln(E_2/\hat{N}_r)/(t - t_r) = \hat{F + M_2}. \quad (34)$$

$$(\hat{u})(\hat{F + M_2})/[1 - e^{-(\hat{F + M_2})(T - t_r)}] = \hat{F}. \quad (35)$$

$$(\hat{F + M_2}) - \hat{F} = \hat{M}_2. \quad (36)$$

$$[\hat{M}_2(T - t_1) + \hat{F}(T - t_r)]/(T - t_1) = \hat{Z}_2. \quad (37)$$

Given $\hat{Z}_2$ from Equation 37, remaining estimates for the case of C known may be calculated in

the following sequence from relations given previously:

Estimate	*Relation*
$\hat{s}_2$	Equation 7
$\hat{N}_1$	Equation 5
$\hat{m}$	Equation 26
$\hat{s}_1$	Equation 1
$\hat{Z}_1 (= \hat{M}_1)$	Equation 8
$(\hat{s_1 s_2})$, $\hat{Z}_T^*$	Equation 6
$\hat{M}_T^*$	Equations 9 and 36

Bias

Equations for bias in $\hat{Z}_T^*$ and in other estimates can be written for the cases of C unknown and known. The equations are much longer than for the Ricker model (e.g., Equations 12-14), however, because estimators from the limit-mean model involve so many substitutions. The equations are therefore not written out but the next section gives numerical examples of bias.

NUMERICAL EXAMPLES OF BIAS

Cleaver's model gives no unique estimators as noted earlier, and it is evident that bias from the Ricker and Fredin models cannot be compared fairly with bias from the limit-mean model when offshore fishing is absent. Thus Equations 10 (Ricker model) and 15 (Fredin model) utilize the information that $M_1 \geq M_{1'} > M_2$ (Ricker, 1962; Parker, 1968), hence $\hat{M}_{1'} = M_{2U}$ as mentioned with Equation 10. For the limit-mean model without offshore fishing, however, it is interesting to see how relative bias differs among the estimates of mortality or survival, maturity, and abundance.

With offshore fishing present and $C > 0$ unknown, we expect $\hat{Z}_2 - Z_2$ or $\hat{Z}_T^* - Z_T^*$ to be less from the Ricker and Fredin models than $\hat{M}_2 - M_2$ or $\hat{M}_T - M_T$ without offshore fishing. For comparisons with bias from the limit-mean model, I use $\hat{Z}_T^* = \hat{Z}_2$ and the resulting $\hat{s}_2$ as the initial estimate for the Ricker model; $\hat{Z}_T^*$ and $\hat{s_1 s_2}$, for the Fredin model. With $C > 0$ known I illustrate bias for the limit-mean model only—again to avoid possibly unfair comparisons with the Ricker and Fredin models.

Data published by Johnson (1970) guided selection of certain hypothetical values for input parameters: the resulting values of E_i/N_0 are intermediate between those he reported for small and large smolts (1964 brood), and in that respect may be typical of coho salmon reared at hatcheries on the lower Columbia River. The value of F assigned here is close to that calculated recently by K.A. Henry of the Northwest Fisheries Center, National Marine Fisheries Service, NOAA, and myself for the 1965-66 brood coho salmon reared at a group of Columbia River hatcheries. All time intervals are accurate to within 1.0 mo and probably to within 0.5 mo as actually

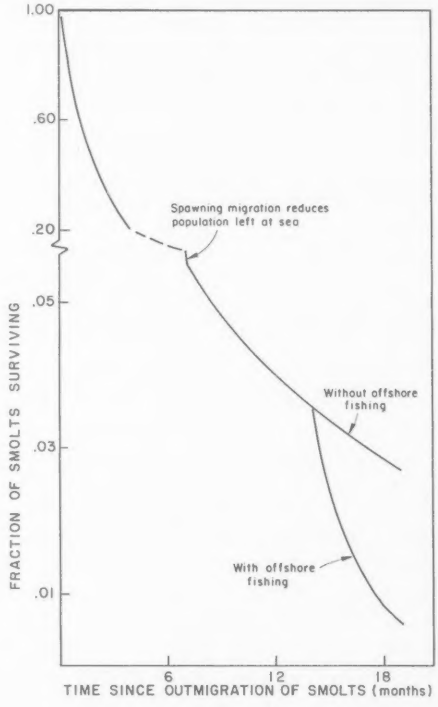

FIGURE 1.—Extinction of a hypothetical smolt class of coho salmon with and without offshore fishing during the last year at sea. Natural mortality is $M_1 = 0.40$/mo during the first $t_1 - t_0 = 7$ mo and 10% of the population matures as jacks; $M_2 = 0.06$/mo during the last $T - t_1 = 12$ mo with or without offshore fishing; and an offshore fishing rate of $F = 0.30$/mo during the last $T - t_r = 5$ mo gives a final population (E_2/N_0, including the inshore catch in both cases) about 22% of that with $F = 0$.

recorded for most coho salmon reared artificially in that watershed. I assume the intervals are known to within 1.0 mo even if $C > 0$ is unknown. Incidentally, all input values are the same as used for Figure 1 to illustrate the extinction of a smolt class with and without offshore fishing.

Table 1 summarizes the hypothetical input values, data, models, assumptions, and estimating schemes as applied to calculate the estimates and values of bias in Table 2. The latter incorporates a few measures to simplify presentation and facilitate comparisons within and between models. Parameter values are repeated from Table 1 and all values are rounded to four places after carrying six in

TABLE 1.—Parameter values, data, models, assumptions, and estimating equations as numbered in text and applied in Table 2 to a hypothetical smolt class of coho salmon.

Parameter value used as input and defined from Equations 1-9		Data	Models, assumptions, and equations
$M_1 = 0.40$/mo	$t_r - t_0 = 14$ mo	$E_1/N_0 = 0.006081$	1. With no offshore fishing ($F = C = 0$), apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20) and $s_{2U} = 0.50$ (Equation 21). Solve Equations 22-27.
$M_2 = 0.06$/mo	$T - t_1 = 12$ mo	$C/N_0 = 0$ (for $F = 0$)	
$F = 0, 0.30$/mo	$T - t_0 = 19$ mo	$C/N_0 = 0.025013$ (for $F = 0.30$)	2. With offshore fishing but $C > 0$ unknown, assume $m = 0$ and $s_2 = 1.0$ on E_1/N_0, hence $\hat{Z}_t = \hat{Z}_T^*$ for Ricker model (Equation 10): use $\hat{Z}_T^*$ to $\hat{Z}_2$, solve Equation 7 for $\hat{s}_2$, then Equation 5 for $\hat{s}_1\hat{s}_2 = E_2/N_0 + (E_1/N_0)\hat{s}_2$, and Equations 24-27. For Fredin model, assume $\hat{Z}_t = \hat{Z}_T^*$ and solve Equations 15 and 22-27. For limit-mean model, proceed as in Item 1 above, noting E_2/N_0 is now smaller.
$Z_2 = 0.185000$/mo (for $F = 0.30$/mo)	$s_1 = 0.060810$	$E_2/N_0 = 0.022640$ (for $F = 0$)	
$M_r^* = 0.230000$/mo	$s_2 = 0.486752$ (for $F = 0$)	$E_2/N_0 = 0.005944$ (for $F = 0.30$)	
$M_T^* = 0.185263$/mo	$s_2 = 0.108609$ (for $F = 0.30$)	Time intervals as at left	3. With offshore fishing and $C > 0$ known, apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20), $M_2 = 0$ during $T - t_r$ (Equation 28) and $F = 0$ during $T - t_r$. Solve Equations 20 and 28-37, then Equations 7, 5, 26, 1, and 6.
$Z_T^* = 0.264211$/mo (for $F = 0.30$/mo)	$s_1 s_2 = 0.029599$ (for $F = 0$)		
$m = 0.10$	$s_1 s_2 = 0.006605$ (for $F = 0.30$)		4. Although $\hat{M}_2$, $\hat{F}$ and $\hat{u}$ are solved only as in Item 3 above, solutions for various mortality coefficients are available from Equations 6-9 by applying survival estimates and $F \geq 0$ as appropriate in Items 1-2 (see section on Actual Situation in text).
$t_1 - t_0 = 7$ mo	$u = 0$ (for $F = 0$)		
$t_r - t_1 = 7$ mo	$u = 0.695584$ (for $F = 0.30$)		
$T - t_r = 5$ mo	$N_1/N_0 = 0.054729$		
	$N_r/N_0 = 0.035960$		

TABLE 2.—Values of parameters, selected estimates, and relative bias in estimates (read each set down in that order), from models as summarized in Table 1. Values are rounded to four places after carrying six in calculations; a dash (—) indicates no estimate.

Offshore fishing	Offshore catch	Model	s_1s_2	s_1	s_2	m	N_1/N_0	N_r/N_0	F	M_2	u
Absent	0	Limit-mean	0.0296	0.0608	0.4868	0.1000	0.0547	0.0360	0.0000	0.0600	0.0000
			0.0286	0.0910	0.3143	0.0668	0.0432	0.0432	—	—	—
			-0.0354	0.4962	-0.3544	-0.3317	0.6060	0.2000	—	—	—
Present	>0, unknown	Ricker	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0063	0.1031	0.0613	0.0590	0.0970	0.0195	—	—	—
			-0.0436	0.6947	-0.4356	-0.4100	0.7719	-0.4588	—	—	—
		Fredin	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0062	0.1536	0.0403	0.0396	0.0475	0.0232	—	—	—
			-0.0629	1.5261	-0.6290	-0.6041	-0.1315	-0.3553	—	—	—
		Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0076	0.0279	0.2726	0.2181	0.0218	0.0102	—	—	—
			0.1510	-0.5414	1.5099	1.1806	-0.6016	-0.7159	—	—	—
Present	>0, known	Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0065	0.0758	0.0852	0.0802	0.0697	0.0383	0.2884	0.0850	0.6526
			-0.0215	0.2468	-0.2152	-0.1979	0.2742	0.0659	-0.0384	0.4165	-0.0617

calculations. Bias is expressed as the ratio, (estimate-parameter value)/parameter value. Values for F, M_2, and u are given for the limit-mean model with $C > 0$ known but values for mortality and bias are not given for the other examples. Values of E_i/N_0 include the inshore catch as if smolts are marked. It should be noted for the last two items that 1) bias in estimated mortality coefficients not shown in Table 1 can be calculated readily from the survival estimates, Equations 6-9, and parameter values in Table 1; and 2) whenever the E_i/N_0 are from spawning areas only, $C > 0$ *and* the inshore catch are unknown but the calculations proceed exactly as in Tables 1 and 2 with lower values of E_i/N_0 which include the effects of inshore fishing (see section on Actual Situation).

Table 2 shows striking contrasts in bias between estimates of different parameters from a given model. The limit-mean model with no offshore fishing, for instance, underestimates the target parameter, s_1s_2, by only 4% but overestimates N_1/N_0 by 61% and N_j/N_0 by 20%. Also in that example, $\hat{s}_2 \simeq 49\%$ is close to the assumed upper limit, $\hat{s}_{2U} = 50\%$ (Table 1); s_2 is 35% too low and $\hat{M}_2 \simeq 0.0965$/mo (calculation from Equation 7 with $F = 0$ not shown) exceeds $M_2 = 0.0600$/mo. Thus $\hat{M}_2 = M_{2U}$ and $(\hat{N}_j/N_0) = (N_j/N_0)_U$ in the example.

With $C > 0$ and unknown, the Ricker model as used here gives smaller bias in estimates of s_1s_2, s_1 and m; the Fredin model as used here, of N_1/N_0 and N_j/N_0; and the limit-mean model, of m. For these and all examples, bias in estimates of s_1s_2, s_2 and m is in the same direction; of the s_i and of s_1 and m, in opposite directions: this result is completely general and is dictated by the fixed relations between these parameters and data (N_0 and E_i) in Equations 1 and 5. Again evident is the wide range of bias values for different parameter estimates within a model: -4% to 77% for the Ricker model, -6% to 153% for the Fredin model, and -72% to 151% for the limit-mean model.

With $C > 0$ known, N_j/N_0 (instead of s_1s_2) is the target parameter (Table 1) and the estimate is 6% too large. In addition to providing the only point estimates shown for F, M_2 and u, the limit-mean model performs better in these examples for the six other parameters than when offshore fishing is absent or when $C > 0$ is unknown. Bias in all six estimates is in the same direction as without offshore fishing and opposite in direction to bias from the limit-mean model with $C > 0$ unknown. Finally, the addition of offshore catch data given the smallest range of bias values for estimates of all six parameters: -22% to 27%.

SUMMARY AND CONCLUSIONS

1. The indirect approach for approximating interval-specific mortality parameters is applicable to multireturn species of salmon when data are available on at least a) the origin-specific number of smolts, b) the origin-specific numbers of adults returning from the sea each year until the smolt class is extinct, and c) the time intervals between seaward migration of smolts and each return. An offshore fishery may or may not exist and the origin-specific catches inshore or offshore may be known (as from marking/recovery experiments) or unknown.

2. Nominally unbiased estimators of mortality (or survival), maturity, and abundance do not exist in this situation because different combinations of mortality and maturity schedules can generate the same set of observable data. In connection with biomass computations, Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969) developed models for approximating interval-specific mortality. The latter three models are reviewed in connection with the problem of bias and a new model is introduced. Observable data are assumed to be accurate in order to focus attention on bias from the models themselves. To sharpen the focus, the problem is reduced to the case of two returns and the pertinent portion of the life history of coho salmon south of British Columbia is emphasized.

3. Equations 1-9 and Figure 1 summarize the actual situation and include the situation with no offshore fishing ($F = C = 0$) to help relate the case of two returns to models developed mainly with data from more returns and, except for Cleaver's model, with natural but

not fishing mortality operating in offshore waters.

4. Mortality estimates from the Ricker (1962) and Fredin (1964) models (Equations 10 and 15, respectively) both utilize for biomass computations the independent evidence that natural mortality coefficients are highest in small, "prerecruit" stages of ocean life and lowest in later stages when fish are large enough to be exploited in offshore as distinct from inshore waters; both models give an average rate of natural mortality which is an upper limit for "prerecruits" and a lower limit for "postrecruits" (quotation marks above indicate these models were developed and applied to hypothetical as distinct from actual offshore fisheries). Ricker's model treats preultimate returns or spawning escapements as if none of those fish mature and all survive until the end of ocean life as observed with the last actual return. Equations 12-14 express absolute bias in mortality estimates from the Ricker model in terms of the unknown maturity parameter and observable data without offshore fishing or with an offshore catch unknown. Fredin's model accounts for actual timing of all returns and therefore approximates more closely than Ricker's model the actual mortality coefficients for any set of data taken when no fishery operates offshore. Fredin's model is solved by trial and error so explicit bias equations cannot be written. When offshore fishing occurs but the origin-specific offshore catch is unknown, it is reasonable to expect from both models less (unknown) bias in mortality coefficients than without offshore fishing; i.e., to use calculated values along with the fixed relations in Equations 1 and 5 as estimates of actual mortality rather than as limits for natural mortality.

5. Biomass computations of Ricker (1962), Parker (1963), and Fredin (1964) overestimate minimum losses in yield. Although the evidence indicates growth typically exceeds mortality in potential and actual postrecruits, the implicit assumption of full availability is in error: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock in offshore waters.

6. Cleaver's (1969) model is the first actually to utilize known offshore catches (but see Equation 7 of Ricker, 1964). Its basic assumption is that natural mortality is absent during the last year of ocean life; the assumption leads to certain one-sided limits, e.g., to the minimum population about a year before the last return (Equations 16-18). The model does not give unique estimators or bias equations but is the basis for the limit-mean model.

7. The limit-mean model with offshore fishing absent or offshore catch unknown assumes a) the survival between times of outmigration and of the first return does not exceed survival between times of the first and second returns (Equations 19-20) and b) the latter survival is less than 1.0 (Equation 21). The result is lower and upper limits on the product of these two survival fractions. The geometric mean of limits is taken arbitrarily as an estimator of the product (Equation 22), then the fixed relations among parameters and observable data (Equations 1-5) give estimates of the survival, maturity, and abundance schedules (Equations 23-27). With an offshore catch known by origin, the first assumption above (Equation 20) gives an upper limit for the number of immatures at sea near the time of the first return (Equations 2 and 29). The additional assumptions of no fishing or natural mortality after recruitment offshore gives lower and upper limits for the number recruited (Equations 28 and 31). The geometric mean is taken arbitrarily as an estimator (Equation 32) to give estimates of the exploitation rate, fishing, and natural mortality coefficients (Equations 33-37). Other estimates for survival, mortality, maturity, and abundance are then available. The limit-mean model involves many substitutions and the cumbersome bias equations are not given.

8. Numerical examples of relative bias for a hypothetical smolt class of coho salmon are explained and presented in Tables 1 and 2. Values are chosen for close agreement with data and estimates for coho salmon actually reared at Columbia River hatcheries. The four examples in Table 2 show a wide range of bias in estimates of different parameters from the same model, and also for the same parameter as estimated from different models in

different situations. Overall performance is best with these hypothetical values for the limit-mean model with offshore catch known, and this model also provides estimates of fishing and natural mortality rates offshore.

9. Direct sampling for maturity in offshore catches, when known by origin, would give nominally unbiased estimators for all parameters but those mentioned last in Item 8 above, and further would permit estimation of survival or mortality during about the last year at sea *without* data on the number of smolts. Although Atlantic salmon caught off Greenland are nearly all immature (Horsted, 1971), it may be recommended for coho and chinook salmon caught off western North America that a) maturity be monitored systematically by time and area and b) research be intensified on determining catch by origin independently of marking smolts (e.g., separating hatchery fish from wild fish by scale patterns).

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LITERATURE CITED

CLEAVER, F. C.
1969. Effects of ocean fishing on 1961-brood fall chinook salmon from Columbia River hatcheries. Fish Comm. Oreg., Res. Rep. 1(1), 76 p.

DOI, T.
1962. Theoretical considerations on rationality of offshore salmon fisheries from the standpoint of effectual utilization of the population. Bull. Tokai Reg. Fish. Res. Lab. 34:1-12.

DRUCKER, B.
1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. Fish. Bull., U.S. 70:79-94.

FREDIN, R. A.
1964. Ocean mortality and maturity schedules of Karluk River sockeye salmon and some comparisons of marine growth and mortality rates. U.S. Fish Wildl. Serv., Fish. Bull. 63:551-574.
1965. Some methods for estimating ocean mortality of Pacific salmon and applications. J. Fish. Res. Board Can. 22:33-51.

FUKUHARA, F. M.
1953. Japanese 1952 North Pacific salmon fishing expedition. Commer. Fish. Rev. 15(2):1-17.

GILBERT, J. R.
1963. Appendix A-3. Research on regulations to provide maximum sustained yield. Rep. *In* R. S. Croaker and D. Reed (editors), Second Governors' Conference on Pacific Salmon, Seattle, Wash., p. 48-50. State Printing Plant, Olympia, Wash.

GODFREY, H.
1965. Salmon of the North Pacific Ocean—Part IX. Coho, chinook and masu salmon in offshore waters. 1. Coho salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 16:1-39.

HENRY, K. A.
1971. Estimates of maturation and ocean mortality for Columbia River hatchery fall chinook salmon and the effect of no ocean fishing on yield. Fish Comm. Oreg., Res. Rep. 3:13-27.
1972. Ocean distribution, growth, and effects of the troll fishery on yield of fall chinook salmon from Columbia River hatcheries. Fish. Bull., U.S. 70:431-445.

HIRSCHHORN, G.
1966. Effect of growth pattern and exploitation features on yields of pink salmon in the northwestern North Pacific. Trans. Am. Fish. Soc. 95:39-51.

HORSTED, S. A.
1971. Det Grønlandske laksfiskeri og debatten omkring det biologisk belyst (The Greenland salmon fishery including a discussion from a biological angle). Grønland, det Grønlandske Selskab 9:257-274. (Transl. Dep. Agric. Fish. Scotland, Mar. Lab., Aberdeen, Transl. 1693.)

JOHNSON, A. K.
1970. The effect of size at release on the contribution of 1964-brood Big Creek Hatchery coho salmon to the Pacific Coast sport and commercial fisheries. Fish Comm. Oreg., Res. Rep. 2(1):64-76.

LANDER, R. H., K. N. THORSON, R. C. SIMON, T. A. DARK, AND G. K. TANONAKA.
1967. Ocean mortality and growth. Int. North Pac. Fish. Comm., Annu. Rep. 1965:99-106.

MASON, J. E.
1965. Salmon of the North Pacific Ocean—Part IX. Coho, chinook and masu salmon in offshore waters. 2. Chinook salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 16:41-73.

MATHEWS, S. B.
1968. An estimate of ocean mortality of Bristol Bay sockeye salmon three years at sea. J. Fish. Res. Board Can. 25:1219-1227.

MURPHY, G. I.
1952. Analysis of silver salmon counts at Benbow

Dam, South Fork of Eel River, California. Calif. Fish Game 38:105-112.

PARKER, R. R.
1960. Critical size and maximum yield for chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 17:199-210.
1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 19:561-589.
1963. On the problem of maximum yield from North Pacific sockeye salmon stocks. J. Fish. Res. Board Can. 20:1371-1396.
1968. Marine mortality schedules of pink sulmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757-794.

PAULIK, G. J., AND D. S. ROBSON.
1969. Statistical calculations for change-in-ratio estimators of population parameters. J. Wildl. Manage. 33:1-27.

RICKER, W. E.
1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Board Can. 19:531-560.
1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Board Can. 21:905-931.

SHAPOVALOV, L., AND A. C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish Bull. 98, 375 p.

TAGUCHI, K.
1961a. A trial to estimate the instantaneous rate of natural mortality of adult salmon (*Oncorhynchus* sp.) and the consideration of rationality of offshore fishing-I. For chum salmon (*Oncorhynchus keta*) 1961. Bull. Jap. Soc. Sci. Fish. 27:963-971. (Transl., Northwest Fish. Center, Natl. Mar. Fish. Serv., Seattle, Wash.)
1961b. A trial to estimate the instantaneous rate of natural mortality of adult salmon (*Oncorhynchus* sp.) and the consideration of rationality of offshore fishing-II. For red salmon (*Oncorhynchus nerka*) 1961. Bull. Jap. Soc. Sci. Fish. 27:972-978. (Transl., Northwest Fish. Center, Natl. Mar. Fish. Serv., Seattle, Wash.)

WORLUND, D. D., R. J. WAHLE, AND P. D. ZIMMER.
1969. Contribution of Columbia River hatcheries to harvest of fall chinook salmon (*Oncorhynchus tshawytscha*). U.S. Fish Wildl. Serv., Fish. Bull. 67:361-391.

THE DISTRIBUTION OF SUMMER FLOUNDER, *PARALICHTHYS DENTATUS*, EGGS AND LARVAE ON THE CONTINENTAL SHELF BETWEEN CAPE COD AND CAPE LOOKOUT, 1965-66

W. G. SMITH[1]

ABSTRACT

Eggs and larvae of summer flounder, *Paralichthys dentatus*, were collected with Gulf V plankton nets between Cape Cod, Mass., and Cape Lookout, N.C., during a 1-year survey of continental shelf waters. The most productive spawning grounds were located off New York and New Jersey. Spawning began in northern parts of the survey area, progressed southward with the season, and ended off Cape Lookout. We collected eggs north of Chesapeake Bay from September to December and south of the Bay from November to February, and larvae north of Chesapeake Bay from September to February and south of the Bay from November to May. Most spawning occurred at temperatures between 12° and 19°C, but the pelagic eggs were caught at mean temperatures from 9.1° to 22.9°C, and the larvae from 0° to 23.1°C.

Fishery scientists generally agree that the shallow, protected waters of bays, rivers, and sounds along our eastern seaboard provide essential habitat for many marine fishes. The occurrence of juvenile fishes in estuaries has led biologists to conclude that a major role of the estuarine zone is its function as a sanctuary or nursery ground for young fishes, many of which are spawned at sea. In 1965, the Sandy Hook Laboratory at Highlands, N.J., began a study to elucidate the degree of estuarine dependence of young fishes by studying their distributions from egg through juvenile stages. Impetus for the study resulted from the accelerated degradation of the estuarine zone and a concurrent decline in some of our most valuable coastal fishery yields.

We began our program with a 1-year survey of the continental shelf between Cape Cod, Mass., and Cape Lookout, N.C., to determine the duration of spawning, define the areas of spawning, and trace the dispersal of pelagic eggs and larvae of all marine sport fishes that we caught. This report describes the offshore distribution of eggs and larvae of the summer flounder, *Paralichthys dentatus*, a highly prized catch for both sport and commercial fishermen.

The life history of summer flounder is understood only in broad outline. The geographic range of the species encompasses estuarine and continental shelf waters from Maine to Florida (Gutherz, 1967). Within this range, the species' population structure remains to be determined. Migratory habits of summer flounder in the Middle Atlantic Bight have been outlined from seasonal changes in the location of commercial and sport catches. From the returns of tagged fish, Poole (1962) and Murawski (1970) added support to the general concept that yearly movements of summer flounder are not extensive. The adults migrate shoreward in spring from wintering grounds near the edge of the continental shelf. They summer in shallow coastal waters and adjacent estuaries and, in the fall, again move offshore. Both Poole and Murawski noted the strong tendency of adult fish to return in subsequent years to the area where they had been tagged. Shortly after the adults begin their fall migration, they begin to spawn, presumably on or near the bottom. Eggs and early larval stages have been found only at sea, and young-of-the-year juveniles only in or near the mouths of estuaries.

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Because young-of-the-year have not been captured at sea, biologists have presumed they cannot survive there and, at an early stage of development, must seek an estuarine habitat. This presumption has been challenged, but not systematically tested.

THE CRUISE SCHEDULE

Eight cruises were completed from December 1965 through December 1966. During each cruise, we planned to sample at 92 stations situated along 14 transects. Transects originated as nearshore as water depths would allow the RV *Dolphin* to enter, and extended seaward to depths near or beyond the 183-m depth contour (Figure 1).

The sequence for sampling transects varied, depending primarily on weather (Table 1). On our first cruise in December, inclement weather forced us to omit the two northernmost transects. We sampled at four additional stations

TABLE 1.—Cruise schedule, sequence of sampling transects, and number of stations occupied during RV *Dolphin* ichthyoplankton survey, 1965-66. Sampling interruptions in excess of 48 hr are shown, whether or not the sampling sequence was affected.

Cruise	Sampling dates	Transect or station sampling sequence	Number of stations
D-65-4	3-15 Dec. 1965	C to P	80
D-66-1	25-26 Jan. 1966	B, A-1 and -2	86
	2- 9 Feb. 1966	C to P	
D-66-3	6- 9 Apr. 1966	A to D	92
	13-16 Apr. 1966	E-1 and -2, F to J-7 to -3	
	19-21 Apr. 1966	J-1 and -2 to P	
	22 Apr. 1966	E-8 to -3	
D-66-5	12-25 May 1966	A to P	92
D-66-7	17-20 June 1966	A to D	92
	22-25 June 1966	L to P	
	25-29 June 1966	K to E	
D-66-10	5-10 Aug. 1966	A to F	92
	21-26 Aug. 1966	G to P	
D-66-11	13-14 Sept. 1966	A and B (except B-3)	30
	17-18 Sept. 1966	B-3, C and D	
D-66-12	28 Sept.-6 Oct. 1966	M, N, L to F, E-1 to -3, D-1 to -3	92
	11-15 Oct. 1966	E-4 to -8, F-8 to -4, C to A	
	20 Oct. 1966	P	
D-66-14	9-14 Nov. 1966	E to J (except F-7, E-8)	92
	15-19 Nov. 1966	P to K, F-7, E-8	
	1- 4 Dec. 1966	D to A	

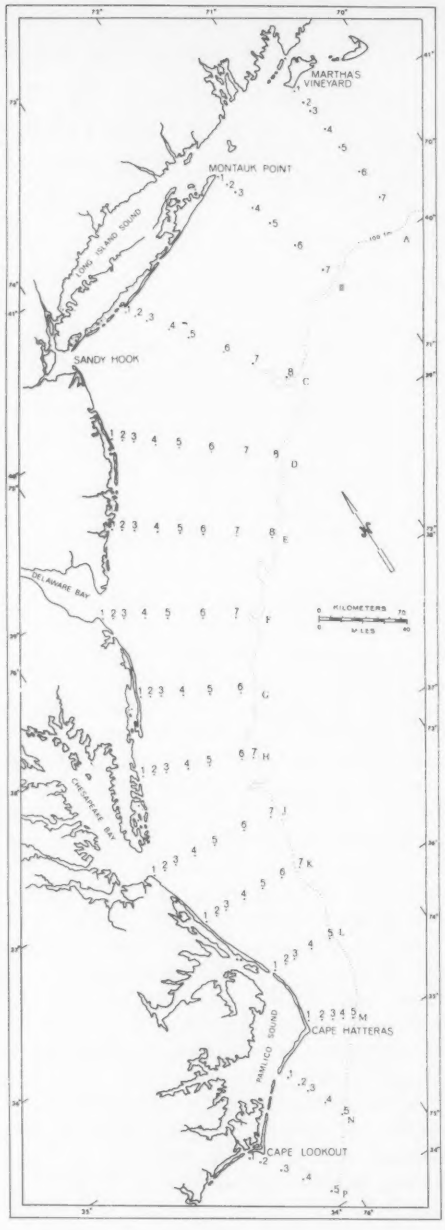

FIGURE 1.—Transects and collecting stations of plankton survey conducted from December 1965 through December 1966.

(designated transect X) off the outer banks of North Carolina. On our second cruise, inclement weather forced us to omit four stations on the northernmost transect, and an outflow of ice from Delaware Bay prevented sampling at the inboard station off Cape Henlopen. We occupied all stations during cruises in April, May, June, and August. In September, adverse weather resulted in a 2-day interruption shortly after we began sampling, and gear problems required a second unscheduled port call soon thereafter. Because of these delays, we rescheduled the cruise after completing only the four northern transects. Although bad weather also interrupted the final two cruises, we occupied all stations.

SAMPLING METHODS

We used Gulf V high speed nets (Arnold, 1959) to collect plankton. These had 0.33-mm Monel[2] wire netting with 12 meshes/cm and a mesh aperture of 0.52 mm.

To assure reaching below the thermocline, or that part of the water column encompassing most pelagic eggs and larvae, we sampled to a maximum depth of 33 m, using two Gulf V nets. One net, hereafter referred to as net no. 1, fished at 3-m depth intervals from surface to 15 m; the other, net no. 2, fished at 3-m depth intervals from 18 to 33 m. We sampled at each depth interval for 5 min. Tows lasted 30 min. In depths less than 33 m, we altered the sampling pattern of net no. 2 by decreasing the number of sampling depth intervals and increasing the towing time at each interval to 10 or to 15 min. Sampling depths for net no. 1 were similarly adjusted in depths less than 15 m (Figure 2). The RV *Dolphin* usually traversed 4.6 km/tow, traveling at a constant engine speed. We preserved plankton samples in 5% buffered Formalin.

Catch per standard tow was used as a measure of relative abundance for eggs and larvae. A standard tow consisted of one or both nets fishing for 5 min at each of the six depth intervals within its vertical sampling range (see Figure 2). The catches were adjusted to equalize sampling effort at all depth levels when either net was limited to sampling at less than six intervals. For example, when only three intervals were sampled during the 30-min tow, the catch was halved. When two intervals were fished, it was reduced by two-thirds. The adjusted catch of net no. 2 was added to that of net no. 1 at stations where both nets fished simultaneously. All catches of eggs and larvae discussed herein are adjusted.

We recorded vertical temperature and salinity data at each station (Clark et al., 1969). Surface temperature was measured with a stem thermometer, subsurface temperature with a mechanical bathythermograph, and salinity with an induction salinometer. Salinity data were recorded at 5-m depth intervals to a maximum depth of 40 m.

Fish eggs and larvae were separated from the plankton collections by microscopically examining aliquots of a sample placed in a gridded Petri dish. Methods employed to check sorting accuracy and measured plankton volumes are described by Clark et al. (1969).

Larvae on which the caudal rays had not formed were measured from the tip of the snout to the tip of the notochord. More developed specimens were measured from the tip of the snout to the base of the median caudal rays. Specimens larger than 9 mm were considered postlarvae because they were laterally flattened. Marginal fin ray counts fell within the adult range and migration of the right eye was underway on specimens over 10 mm.

THE SEASONAL DISTRIBUTION OF EGGS

We sampled during parts of two different spawning seasons, for our survey started too late in 1965 and ended too early in 1966 to determine the beginning of the one season or the end of the other. In spite of the possibility of year-to-year variations in the onset and duration of spawning, data for the 2 years were combined and treated as a single complete season.

Although the summer flounder's spawning

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

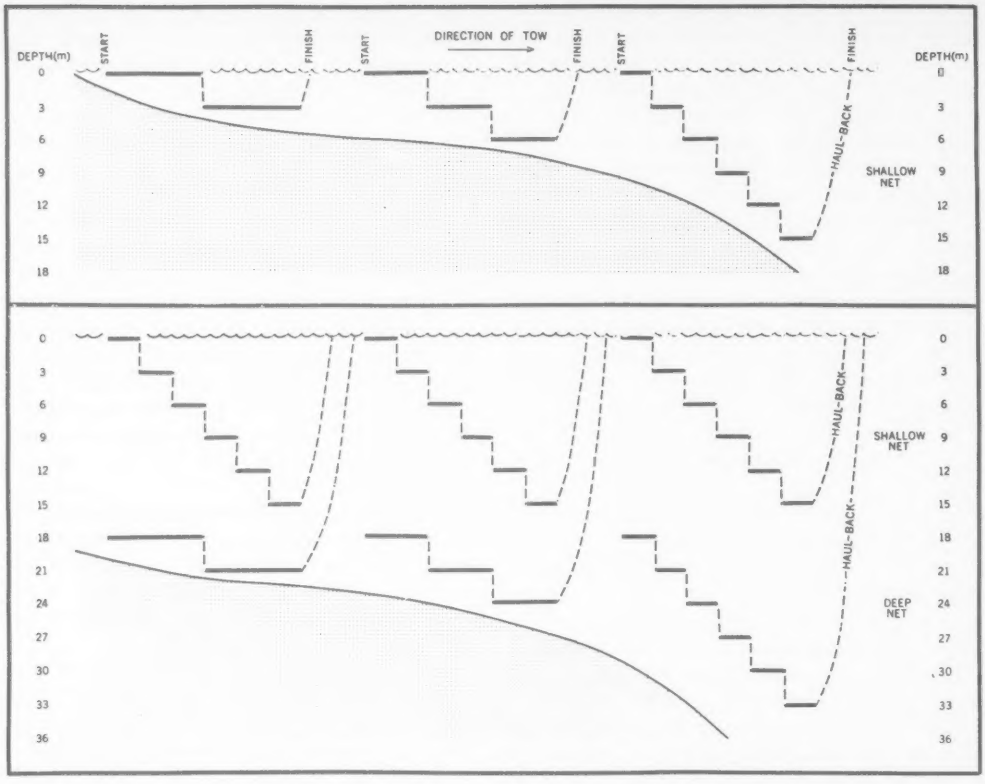

FIGURE 2.—Vertical sampling profiles for 30-min tows with Gulf V nets. The number of sampling depths in the step-oblique pattern was determined by depth of water. Sampling profiles on the right side of the figure were considered standard tows.

season usually peaks in the fall along the Middle Atlantic Bight, data are lacking on the duration of the season. Herman (1963) reported the earliest seasonal occurrence of young from larvae captured in Narragansett Bay, R.I., in July 1957. He concluded that spawning had commenced during the summer. Gravid females taken as late as mid-April off Nantucket Island led Bigelow and Schroeder (1953:267-270) to conclude that spawning occurred through spring. During our survey, it appears that some spawning may have lingered into early spring in waters off North Carolina, but not as far north as New England. Nor can I find other data to substantiate that spawning normally begins as early as July or ends as late as April off southern New England.

After studying gonads from fishes landed by the winter trawl fishery, Eldridge (1962) concluded that most spawning off the Virginia Capes occurred in November. Eldridge's findings agree closely with those of Murawski (1965), who observed a sharp rise in maturation of gonads in fish caught off New Jersey during the first half of October and running ripe females from late September through early November. Our results generally agree with these authors. In 1966, spawning evidently began in the northern part of the Middle Atlantic Bight in early September, progressed southward with the season, and ended in February off Cape Lookout. The season reached its peak in October north of Chesapeake Bay and in November south of the Bay.

We first caught eggs in mid-September. Most of these were 9 to 19 km off western Long Island where depths were 22 to 31 m (Figure 3). Because this September cruise was cancelled after sampling only the four northernmost transects, the data do not show the full distribution of eggs within the area we normally surveyed. Results of the following cruise, however, suggest that spawning in the first half of September was limited to the area between southern New England and New Jersey.

All eggs caught in October were at stations north of Chesapeake Bay, most of them off New Jersey and Delaware. Stations 22 to 61 km offshore over depths of 20 to 48 m accounted for 96% of the catch. No eggs were caught south of Chesapeake Bay (Figure 4).

In November, the area of spawning had moved southward, for concentrations of eggs were now 65 km east of Assateague Island, Md., and 9 to 19 km off the outer banks of North Carolina. Ten days elapsed from the time we started sampling off Atlantic City until we were able to sample the four northern transects. During that period, spawning apparently ended off New York and southern New England, for we caught only one egg in that sector (Figure 5). Considering the substantial number of larvae taken on the four northern transects, it seems probable that the distribution of eggs at the outset of the cruise in November extended further north than shown in Figure 5, perhaps as far as Martha's Vineyard or beyond.

By December (1965), spawning within most of the survey area had ended, for we found eggs only at stations in the southern portion (Figure 6). The following cruise in late January and early February proved even less productive. We caught four eggs at the most southerly station off Cape Lookout. Eggs were absent from samples taken on cruises in April, May, June, and August.

VERTICAL DISTRIBUTION OF EGGS

Our sampling program was not designed to study the vertical distribution of eggs and larvae. The patterns of distribution, however, suggest that summer flounder eggs drift largely within the shallow depths sampled by net no. 1. At stations where both nets fished, net no. 1 caught 75% of the eggs and net no. 2 probably caught some of the remaining 25% in the upper levels during setting and retrieval. This tendency of summer flounder eggs to float near the surface was observed during a rearing experiment set up to obtain early larval stages. All artificially fertilized eggs floated in water collected from just beneath the surface, or in the least dense part of the water column, at the site where gravid adults presumably would have spawned soon thereafter. By floating near or at the surface, the eggs were available to our nets for only a part of the 30-min tow. A short incubation period, 72 to 75 hr after fertilization at an average water temperature of 17.5°C (Smith and Fahay, 1970), may also affect the availability of eggs by limiting their dispersion away from the spawning site. Thus, the buoyancy of eggs and their relatively short incubation period probably account for our nets catching fewer eggs than larvae.

THE SEASONAL DISTRIBUTION OF LARVAE

Judging from the changes in the number of eggs in our samples, summer flounder spawned north of Chesapeake Bay from September to December and south of the Bay from November to February. As expected, larvae were taken at the same time as the eggs, and also over a longer period. We caught larvae in the northern half of the survey area from September to February, and in the southern half from November to May.

Larvae as well as eggs of the 1966 brood appeared first in our collections of mid-September, when we sampled only the four northernmost transects (Figure 3). The small number and size of larvae collected then, the more widespread distribution of eggs than larvae, and the absence of both in June and August all indicate that spawning had recently started, probably during the first week of September. The October cruise produced the largest catch of summer flounder larvae of the survey. All larvae were caught north of Chesa-

peake Bay, some as far as 111 km offshore, but most from 22 to 83 km offshore over depths of 31 to 57 m. Although the distribution of larvae was continuous, distinct concentrations occurred off Martha's Vineyard, off Long Island and northern New Jersey, and off Delaware Bay (Figure 4). By November, the distribution of larvae had spread throughout the survey area, apparently with a center of concentration 56 km off New Jersey, where water depths ranged from 22 to 53 m (Figure 5).

In December (1965), we found concentrations of larvae off New Jersey and North Carolina. The area of greatest abundance was 37 to 83 km off the New Jersey coast, at about the same location where we found larvae most abundant during the November (1966) cruise (Figure 6). By the end of January, the number of larvae and the area of their distribution had diminished, most of them being south of Cape Hatteras (Figure 7). In April, we found larvae only in the southern extreme of the survey area (Figure 8). In May, we caught seven larvae which probably represented remnants of late spawning off the outer banks of North Carolina, since we found no more during the next two cruises.

The seasonal progression of spawning from north to south, evident from the distribution of eggs and larvae, was further substantiated by the progressively smaller larvae that were caught as we sampled southward on late fall and winter cruises. In September, the newly spawned larvae were confined to a small area off western Long Island and northern New Jersey. By October, larvae were distributed over almost the entire northern half of the survey area. In November, when they were spread throughout the survey area, those south of Delaware Bay were smaller than those north of the Bay. In December (1965), larvae generally were largest north of Delaware Bay, and progressively smaller at more southerly stations, the smallest occurring south of Cape Hatteras. Those south of Cape Hatteras in February were small and newly hatched, while most of those to the north had started to metamorphose. By April, when larvae were found only south of Cape Hatteras, most had started to metamorphose (Appendix Table 1).

THE RELATION OF SPAWNING TO WATER TEMPERATURES

Spawning occurred principally within a temperature range of 7°C during the year of our survey. Over the whole season, we caught 77% of the eggs where bottom temperatures were between 12° and 19°C. This percentage would probably be higher if some dispersion by coastal circulation were taken into account. Miller (1952)[3] found surface water drifting from 6 to 37 km/day within the survey area. A minimal drift of 9 km daily would be sufficient to place the origin of 98% of the eggs we caught in bottom waters between 12° and 19°C. There was no evidence that salinity had any effect on the distribution of eggs or larvae.

At the beginning of the season, in September, the summer thermocline remained intact. Water temperatures at the surface and bottom differed by as much as 14.6°C. The greatest concentration of eggs was located off Long Island, shoreward of the cold mass of bottom water that persists during the summer months from New York to as far south as Chesapeake Bay (Bigelow, 1933). Where eggs were most abundant at the surface, bottom temperatures were between 18° and 19°C (Figure 9). The few eggs caught seaward of the cold bottom water might have been spawned by a group of fish that either had migrated from northerly waters around the outer edge of the cold bottom water or by a group that remained in deep water throughout the year. By October, the thermocline was less pronounced than in September, and most of the eggs occurred over bottom temperatures between 13° and 17°C (Figure 9). As in September, the seaward distribution of eggs appeared restricted by the cold mass of bottom water which remained intact off Long Island and New Jersey. It seems certain, therefore, that the inshore edge of the cold water delimited the seaward extent of the fall migration of spawning fish.

[3] Miller, A. R. 1952. A pattern of surface coastal circulation inferred from surface salinity-temperature data and drift bottle recoveries. Woods Hole Oceanogr. Inst. Ref. No. 52-58, 14 p. (Unpubl. manuscr.)

By so doing, the mass of cold water may play a major role in the success or failure of spawning off the Middle Atlantic States, depending on the time when it becomes mixed with surrounding water by late summer and fall storms.

By November, water was mixed and temperatures uniform from surface to bottom, except at those stations on the seaward end of transects. Eggs occurred in greatest numbers off northern Virginia, over 11.7°C bottom water, and off the outer banks of North Carolina, where the bottom temperature was 15.0°C. The northern limit of the principal area of distribution was along the transect off Great Egg Inlet, N.J., where we started the cruise. At that time, bottom temperatures exceeded 12°C (Figure 10). By the time we began sampling the four northernmost transects (see Table 1), bottom temperatures had fallen below 12°C and spawning had practically ended in the northern part of the survey area. It continued in the southern part, where in December (1965) we caught eggs over bottom temperatures of 12° to 19°C (Figure 10). By late January, bottom temperatures were less than 12°C at all but five stations, and we caught eggs only at the most southerly one, where the bottom temperature was 17.8°C.

Presuming that spawing occurs on the bottom, it is limited to a narrow temperature range. The eggs, however, which subsequently rise, are evidently more temperature tolerant than their spawning parents, for we found them at water temperatures as cold as 9.1°C and as warm as 22.9°C, though mostly from 13.0° to 17.9°C. Judging from the hatching time for artificially fertilized eggs, reported by Smith and Fahay (1970), those taken offshore in 9.1°C water required about 142 hr to hatch; those taken at 22.9°C, only 56 hr. Most of the eggs collected during the survey would have hatched 74 to 94 hr after fertilization. Although larvae occurred over a still wider mean temperature range than eggs (0° to 23.1°C), they were most abundant at mean temperatures of 9.0° to 17.9°C (Appendix Table 2). Other workers also have captured young summer flounder over a wide range of both temperature and salinity. Williams and Deubler (1968) caught postlarvae in Pamlico Sound water ranging in temperature from 2° to 22°C and in salinity 0.02 to 35.0‰. Tagatz and Dudley (1961) caught young of 11 to 180 mm in length at temperatures between 9.4° and 31.2°C and salinities between 8.7 and 37.0‰, and Deubler and White (1962) kept post larvae for 33 days in water with a salinity of 40‰.

GEOGRAPHICAL SPAWNING AREAS AND SPAWNING POPULATIONS

Although summer flounder occur occasionally as far north as Maine and as far south as Florida, fishing records indicate that they are most abundant from Cape Cod to Cape Lookout. Thus, it is doubtful that much spawning occurred north or east of our northernmost transect. The most important spawning grounds within the survey area were off New York and New Jersey. We caught the greatest numbers of eggs within 46 km of shore. Larvae were most abundant 22 to 83 km offshore. In some instances, we caught the young stages at our most seaward stations, but, considering the known offshore range of adults, it is unlikely that significant numbers of eggs or larvae occurred beyond our outermost stations. The numbers of eggs and larvae were relatively low off Virginia, increased off the outer banks of North Carolina, and declined off Cape Lookout (Appendix Table 3). Cape Lookout, however, should not be considered the southern limit of spawning, for we caught larvae as far south as Daytona Beach, Fla., in January 1968. Plankton collections south of Cape Lookout in 1953, 1954, and 1967[4] contained summer flounder larvae (Figure 11). More sampling is needed to assess the importance of spawning grounds south of Cape Lookout.

Although research on summer flounder has been sporadic and limited in geographic scope, there is mounting evidence that separate spawning populations exist. The occurrence of distinct areas of egg and larvae abundance at different times of the spawning season; the tag returns of Poole (1962) and Murawski (1970), indicating a general inshore-offshore

[4] Unpublished data on file at Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service, Highlands, N.J. 07732.

movement and a strong tendency of fish to return in subsequent summers to the same area; the short time between departure from the inshore summering grounds and the onset of spawning, which would limit prespawning movement; and, finally, the differences in gill raker and anal ray counts between summer flounder collected at Chesapeake Bay and at Beaufort, N.C. (Ginsburg, 1952) strongly suggest the likelihood of different populations. Judging from our survey in 1965-66, one segment of the species appeared to spawn principally north of Delaware Bay, a second from Virginia to Cape Hatteras, and a third south of Cape Hatteras. The biological evidence is supported by commercial landings. The catch from ports between Maryland and Massachusetts declined by 66% from 1960 through 1967. During the same period, Virginia landings fluctuated but a decline was not evident. In North Carolina, landings increased. If effort remained relatively constant along the coast, it is unlikely that such trends would have occurred if the various coastal fisheries depended on one population.

LARVAL MOVEMENTS

The net transport of water along the Middle Atlantic Bight is generally southerly to southwesterly in the fall (Bumpus and Lauzier, 1965; Norcross and Stanley, 1967). Although pelagic eggs and early larval stages drift in sea currents, it appears that the summer flounder larvae we collected had not drifted far from the spawning areas. Larvae of all stages of development caught off New York and New Jersey, and off North Carolina, were taken in the general vicinity of the eggs (Figures 12 to 16). Although there is no evidence to relate the movement of young summer flounder to known current patterns, early juvenile stages have been captured only in estuaries, suggesting that the young fish are estuarine dependent. Their tolerance to wide ranging temperatures and salinities further suggests that they are physiologically adapted to utilize the estuarine zone for nursery grounds. Judging from our collections and the size of specimens collected at inlets along the coast, the shoreward migration begins after the young fish metamorphose and become capable swimmers.

Most of the postlarvae in our collections were caught at night. Of the 114 specimens larger than 9 mm, 91 (80%) were taken after dark. Additional sampling with modified collecting gear should confirm whether the significantly greater nighttime catch resulted from net avoidance during the day or from diel movements of the metamorphosing young fish. Arnold (1969) noted that metamorphosing postlarvae of the European plaice, *Pleuronectes platessa*, may go quickly to the bottom when not actively swimming. Pearcy (1962) made a similar observation on winter flounder, *Pseudopleuronectes americanus*, considering both the small and large larvae to be partially benthic animals. If postlarval summer flounder behave similarly to the above postlarval flatfishes, then perhaps day-night differences in the catch may reflect periods of low and high activity rather than net avoidance. In this case, the postlarvae would be largely unavailable to our nets when not swimming, which they might do mostly at night. If, on the other hand, the difference between day and night catches reflects net avoidance, towing speeds in excess of 9.3 km/hr are required to adequately sample postlarval summer flounder when using nets with a mouth opening comparable to a Gulf V.

ACKNOWLEDGMENTS

I thank L. A. Walford for his many helpful suggestions during the course of the survey, and for critically reviewing the manuscript; and Elmer J. Gutherz, National Marine Fisheries Service, Pascagoula, Miss., for providing the additional data on larval summer flounder catches south of Cape Lookout.

LITERATURE CITED

ARNOLD, E. L., JR.
1959. The Gulf V plankton sampler. *In* Galveston Biological Laboratory fishery research for the year ending June 30, 1959, p. 111-113. U.S. Fish Wildl. Serv., Circ. 62.

ARNOLD, G. P.
1969. The orientation of plaice larvae (*Pleuronectes platessa* L.) in water currents. J. Exp. Biol. 50:785-801.

BIGELOW, H. B.
1933. Studies of the waters of the Continental Shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. Pap. Phys. Oceanogr. Meteorol., Mass. Inst. Tech. Woods Hole Oceanogr. Inst. 4:1-135.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53:577 p.

BUMPUS, D. F., AND L. M. LAUZIER.
1965. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Ser. Atlas Mar. Environ. Am. Geogr. Soc. Folio 7, 8 plates, [4] p.

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. Data Report I: Northern section, Cape Cod to Cape Lookout. R. V. *Dolphin* cruises 1965-66: zooplankton volumes, midwater trawl collections, temperatures and salinities. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 28, 132 p.

DEUBLER, E. E., JR., AND J. C. WHITE, JR.
1962. Influence of salinity on growth of postlarvae of summer flounder, *Paralichthys dentatus*. Copeia 1962:468-469.

ELDRIDGE, P. J.
1962. Observations on the winter trawl fishery for summer flounder, *Paralichthys dentatus*. M.S. Thesis, Coll. William and Mary, Williamsburg, Va., 55 p.

GINSBURG, I.
1952. Flounders of the genus *Paralichthys* and related genera in American waters. U.S. Fish Wildl. Serv., Fish. Bull. 52:267-351.

GUTHERZ, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Fish Wildl. Serv., Circ. 263, 47 p.

HERMAN, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.

MURAWSKI, W.
1965. Fluke investigations. N.J. Fed. Aid Proj. F-15-R-6 (Completion Rep. Job 3). N.J. Dep. Conserv. Econ. Dev., 21 p.
1970. Results of tagging experiments of summer flounder, *Paralichthys dentatus*, conducted in New Jersey waters from 1960 to 1967. N.J. Dep. Environ. Prot., Misc. Rep. 5M, 72 p.

NORCROSS, J. J., AND E. M. STANLEY.
1967. Circulation of shelf waters of the Chesapeake Bight. II. Inferred surface and bottom drift, June 1963 through October 1964. Environ. Sci. Serv. Adm., Prof. Pap. 3:11-42.

PEARCY, W. G.
1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). II. Distribution and dynamics of larvae. Bull. Bingham Oceanogr. Collect. Yale Univ. 18(1):16-37.

POOLE, J. C.
1962. The fluke population of Great South Bay in relation to the sport fishery. N.Y. Fish Game J. 9:93-117.

SMITH, W. G., AND M. P. FAHAY.
1970. Description of eggs and larvae of the summer flounder, *Paralicthys dentatus*. U.S. Bur. Sport Fish. Wildl., Res. Rep. 75, 21 p.

TAGATZ, M. E., AND D. L. DUDLEY.
1961. Occurrence of marine fishes at four shore habitats near Beaufort, N. C., 1957-60. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 390, 19 p.

WILLIAMS, A. B., AND E. E. DEUBLER.
1968. A ten-year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27-41.

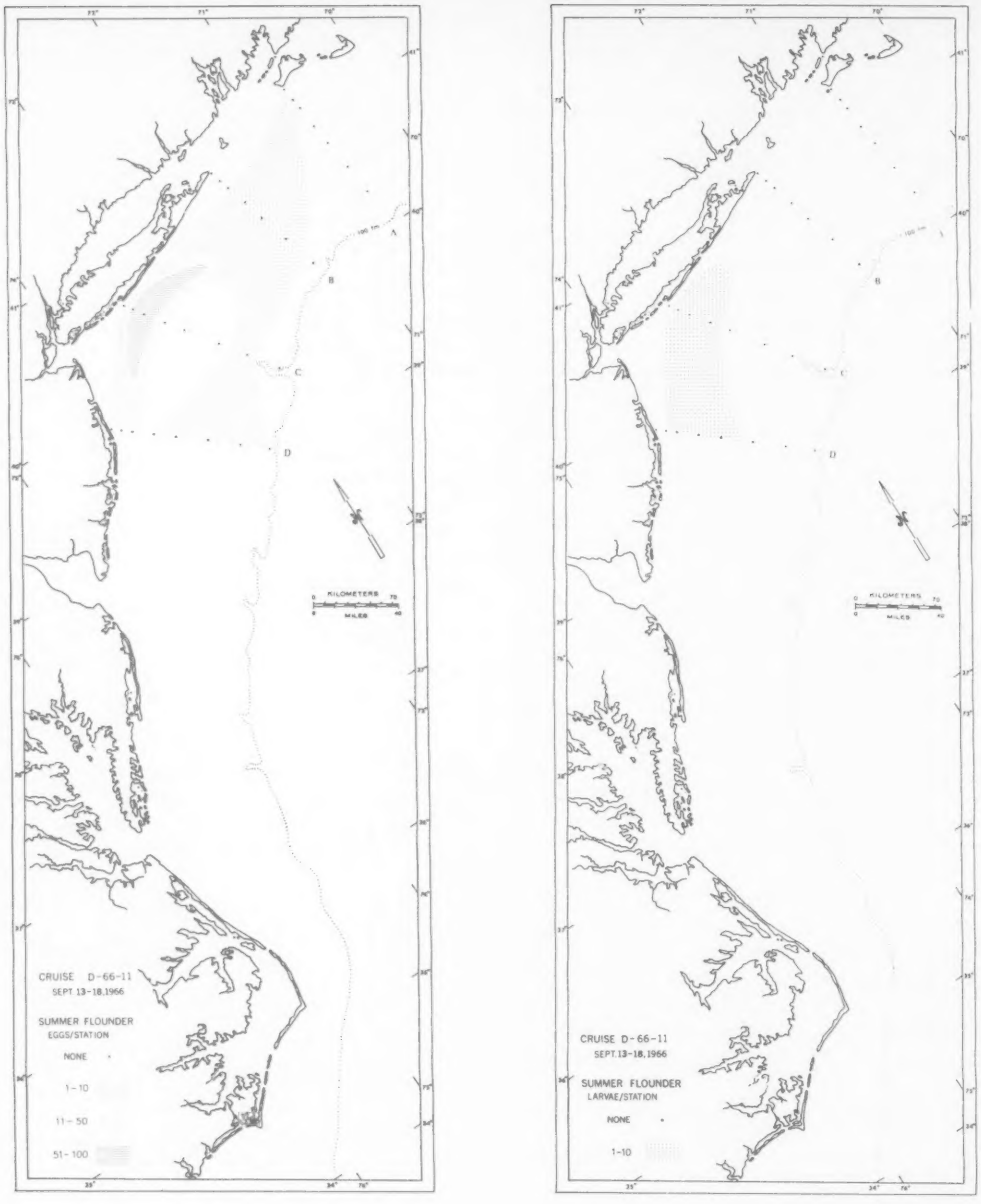

FIGURE 3.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-11.

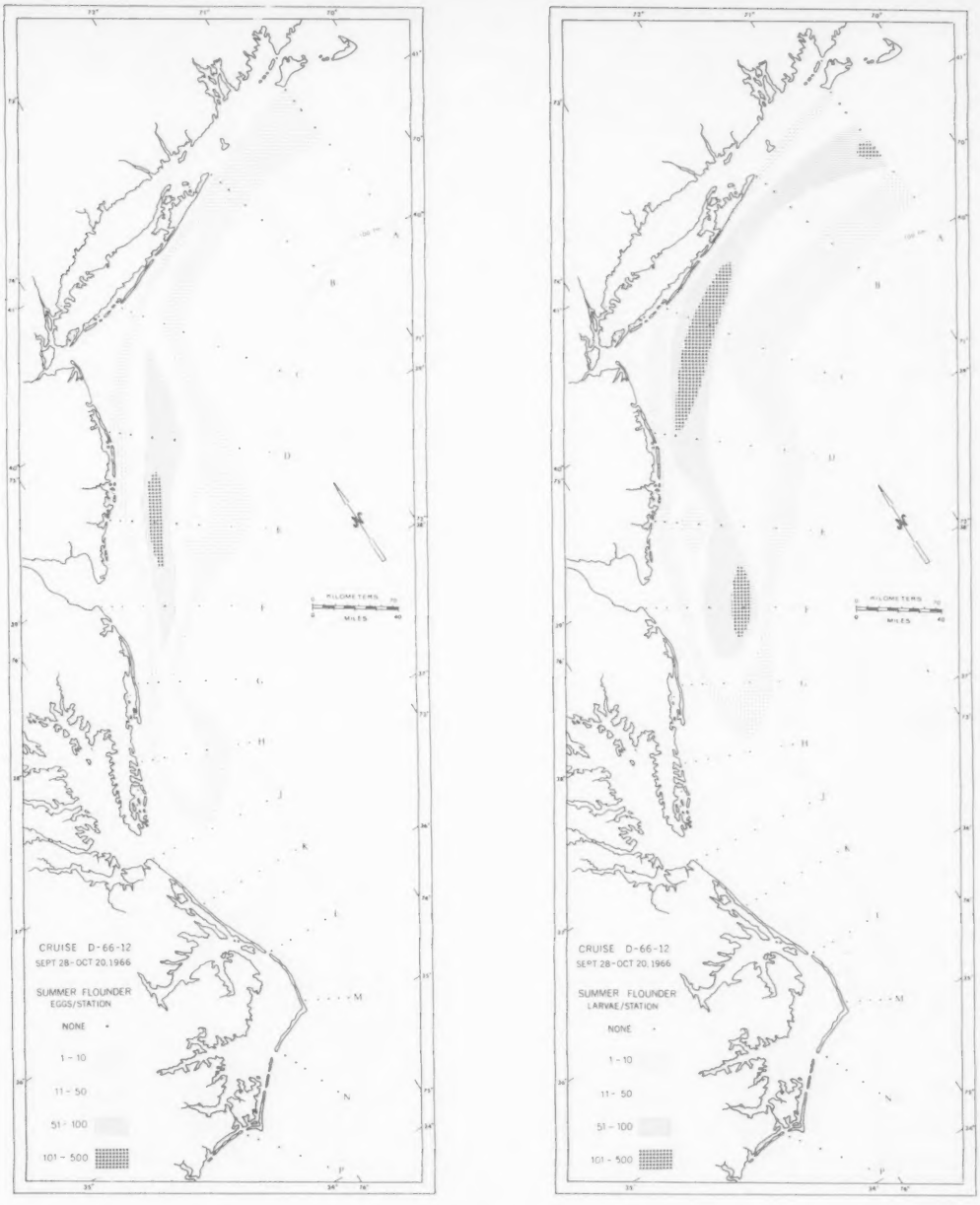

FIGURE 4.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-12.

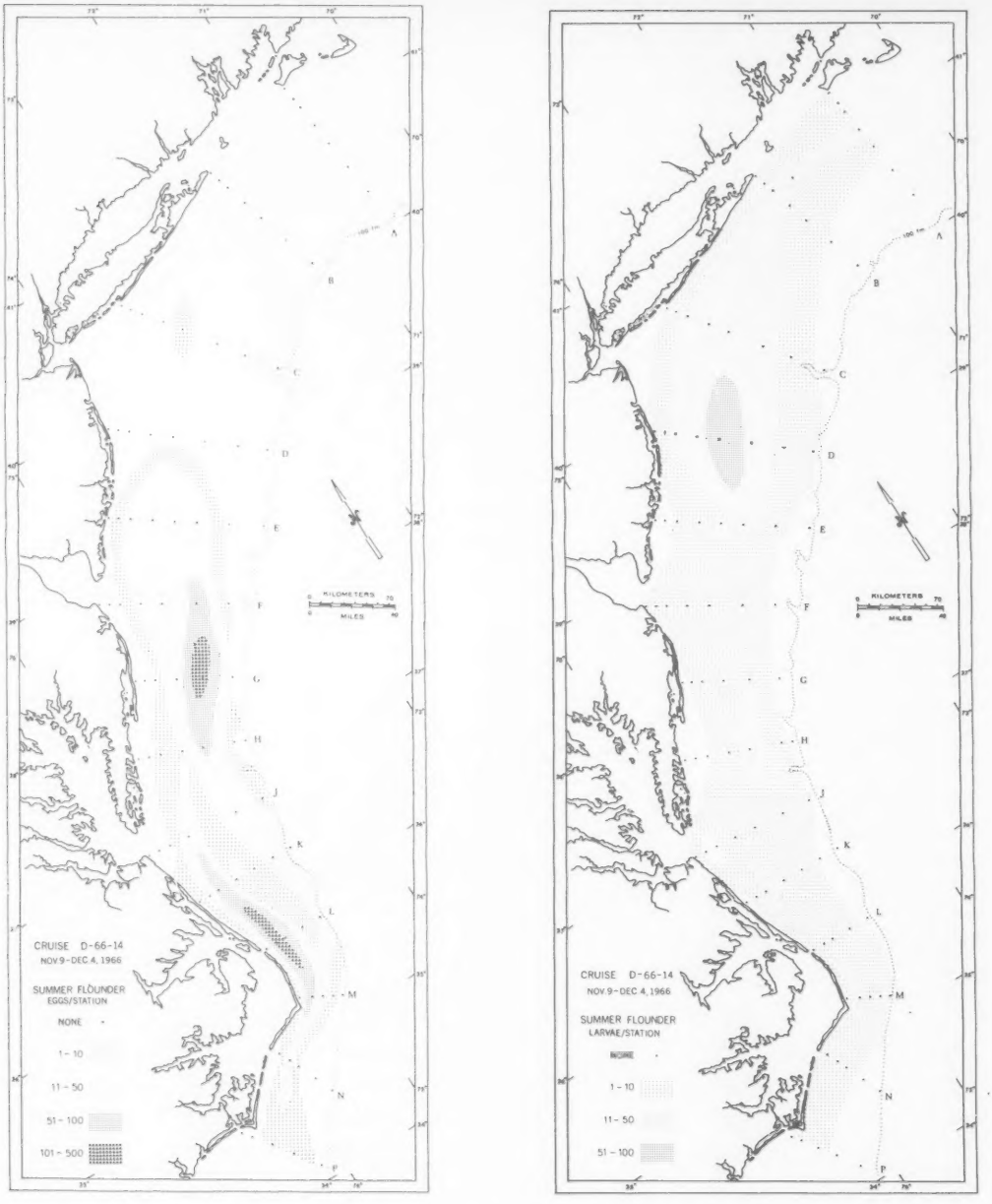

FIGURE 5.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-66-14.

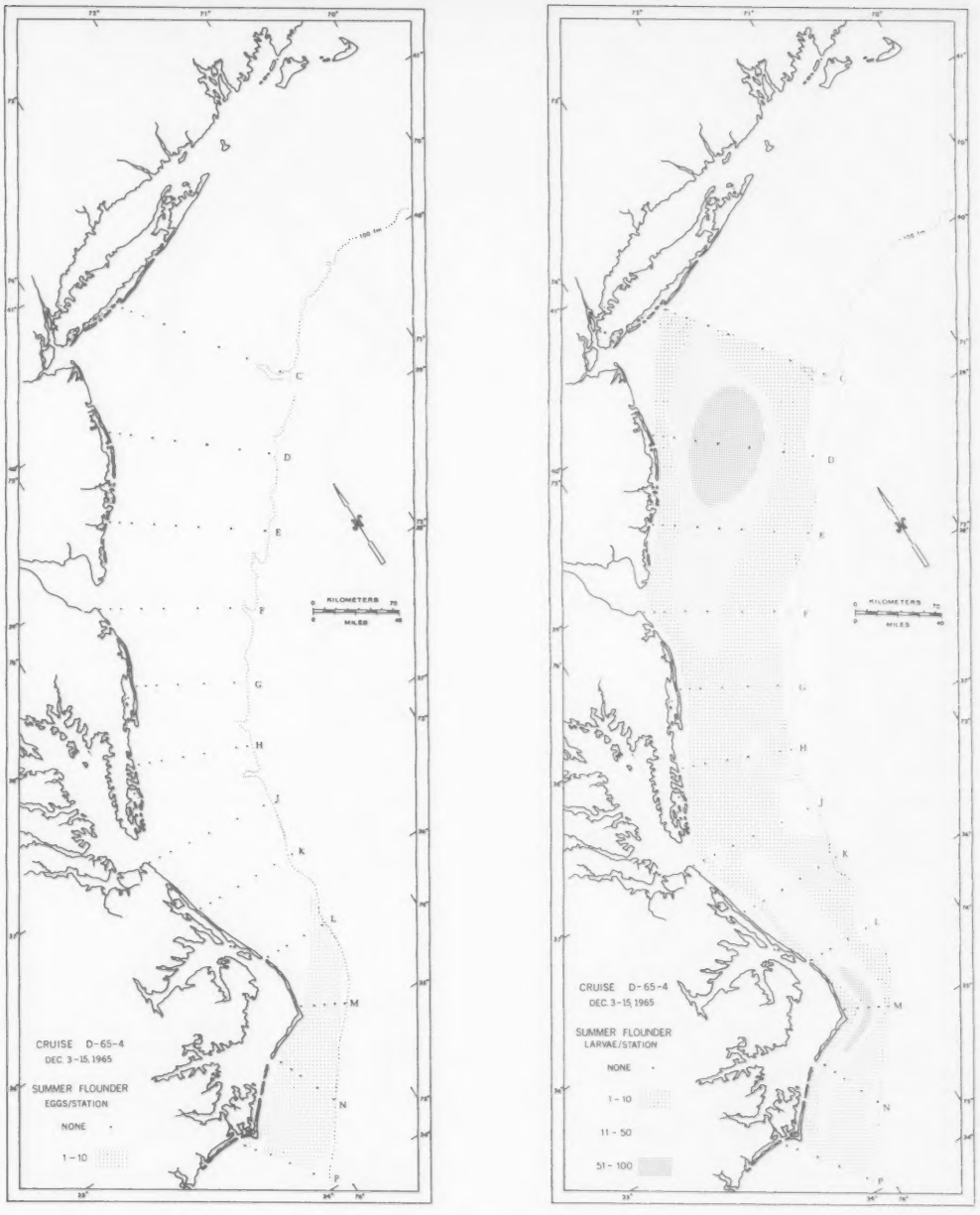

FIGURE 6.—Distribution and relative abundance (adjusted) of summer flounder eggs (left) and larvae (right) from Cruise D-65-4.

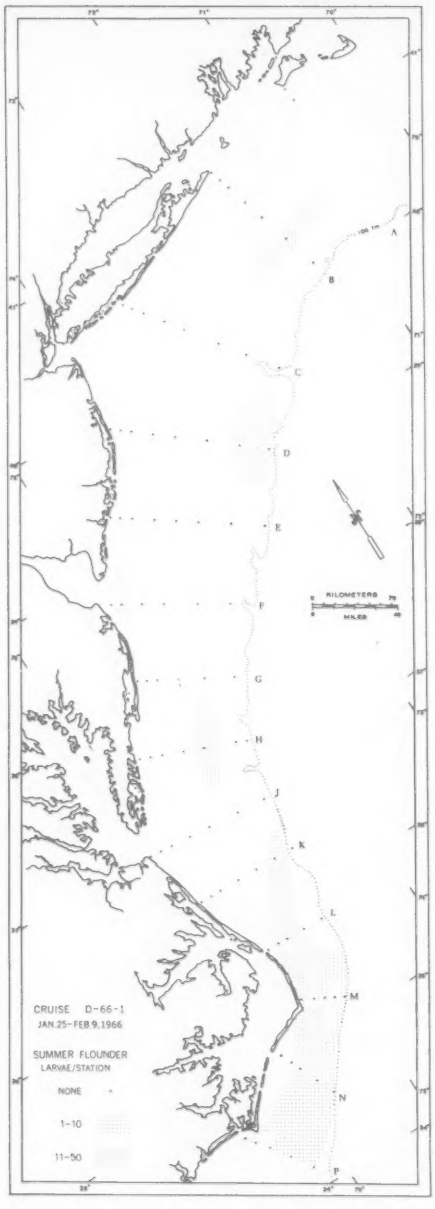

FIGURE 7.—Distribution and relative abundance (adjusted) of summer flounder larvae from Cruise D-66-1.

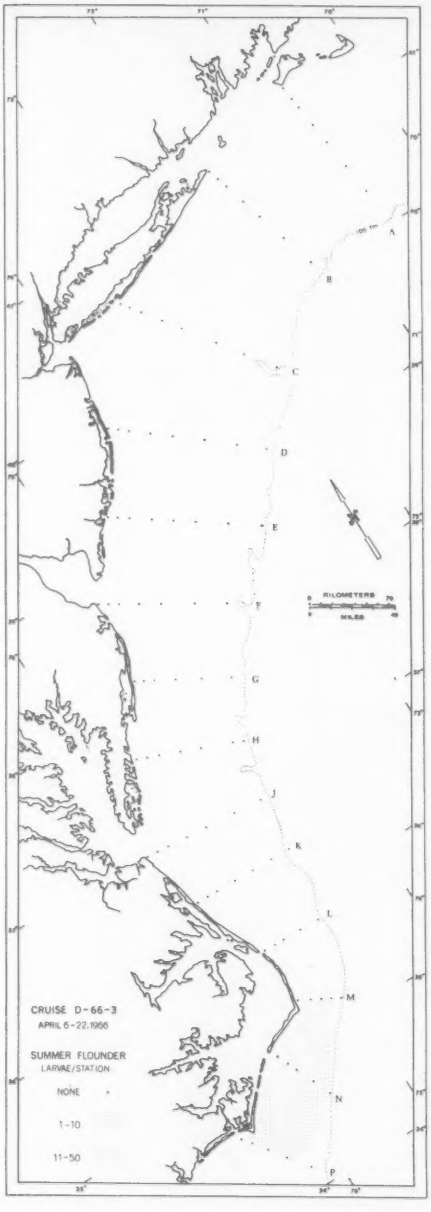

FIGURE 8.—Distribution and relative abundance (adjusted) of summer flounder larvae from Cruise D-66-3.

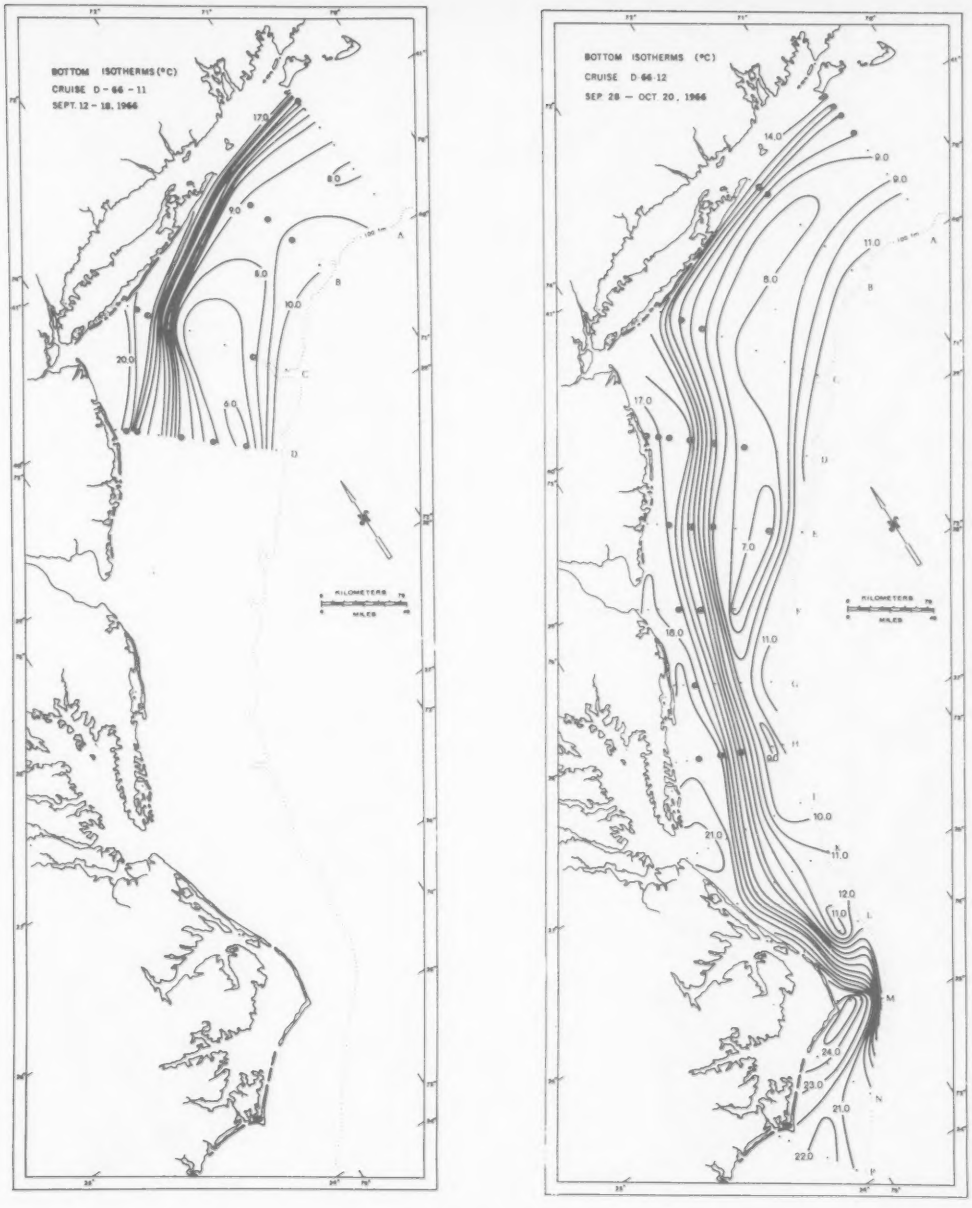

FIGURE 9.—The occurrence of pelagic eggs of summer flounder and associated bottom temperatures from Cruise D-66-11 (left) and Cruise D-66-12 (right). Eggs occurred at station positions shown by a large dot.

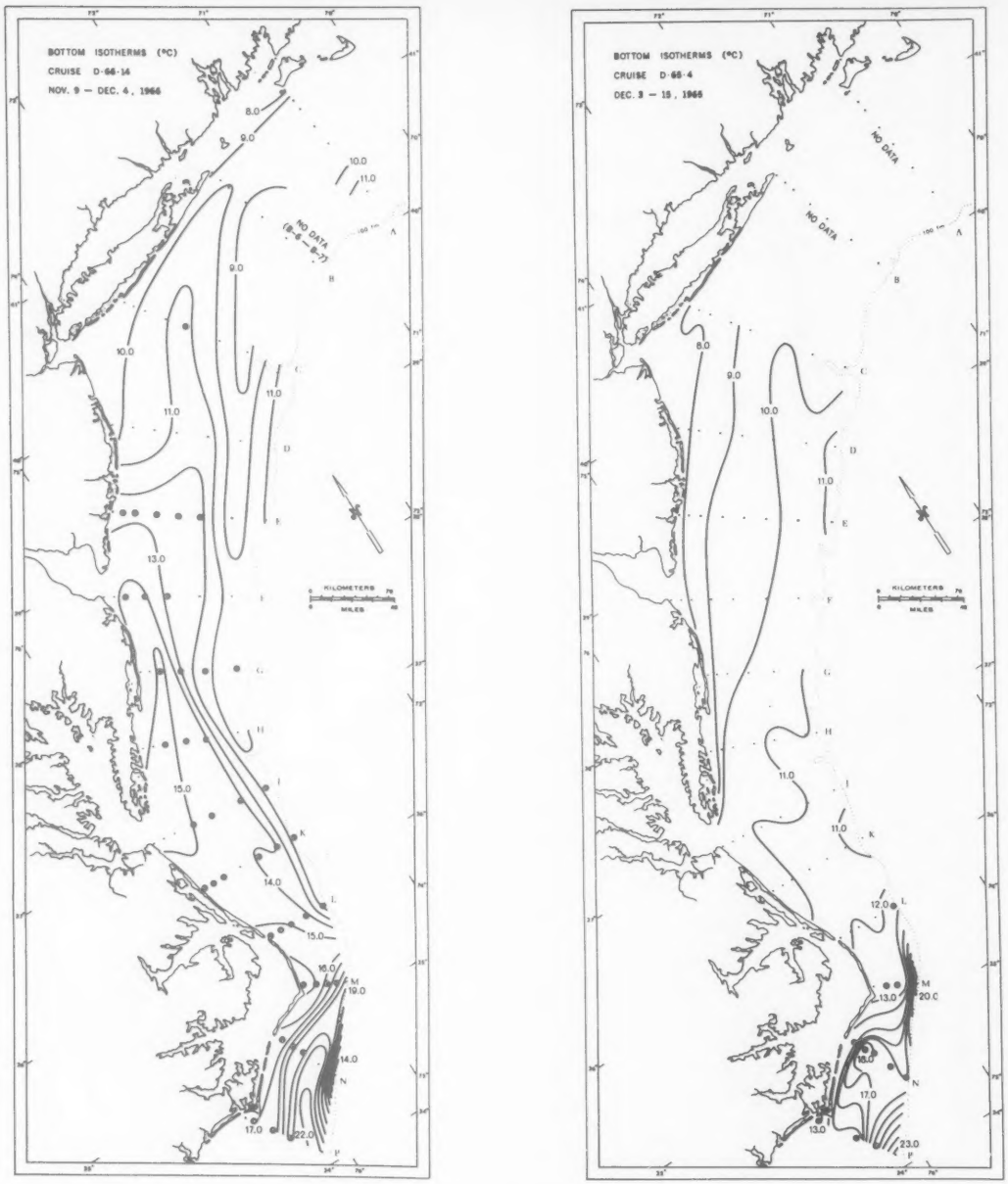

FIGURE 10.—The occurrence of pelagic eggs of summer flounder and associated bottom temperatures from Cruise D-66-14 (left) and Cruise D-65-4 (right). Eggs occurred at station positions shown by a large dot.

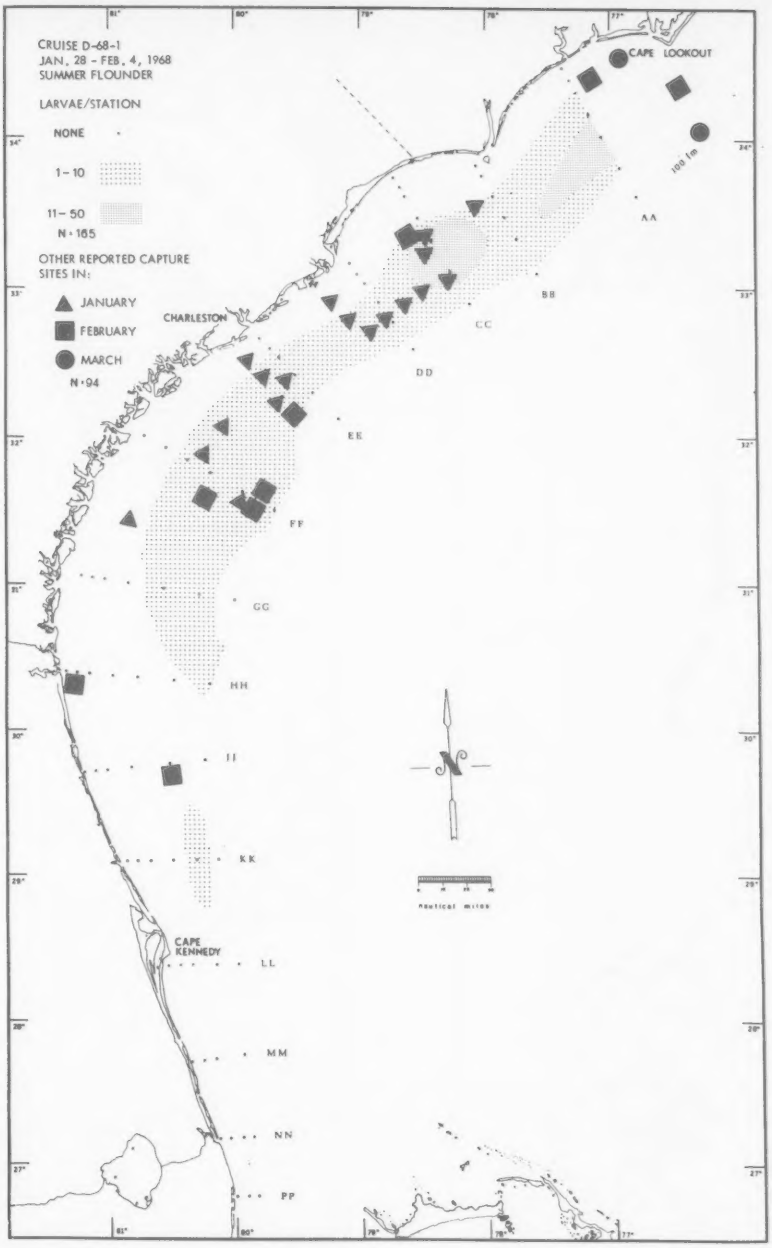

FIGURE 11.—Distribution and relative abundance of summer flounder larvae captured by RV *Dolphin* between New River, N.C., and Palm Beach, Fla., in 1968, and other reported capture sites of summer flounder larvae.

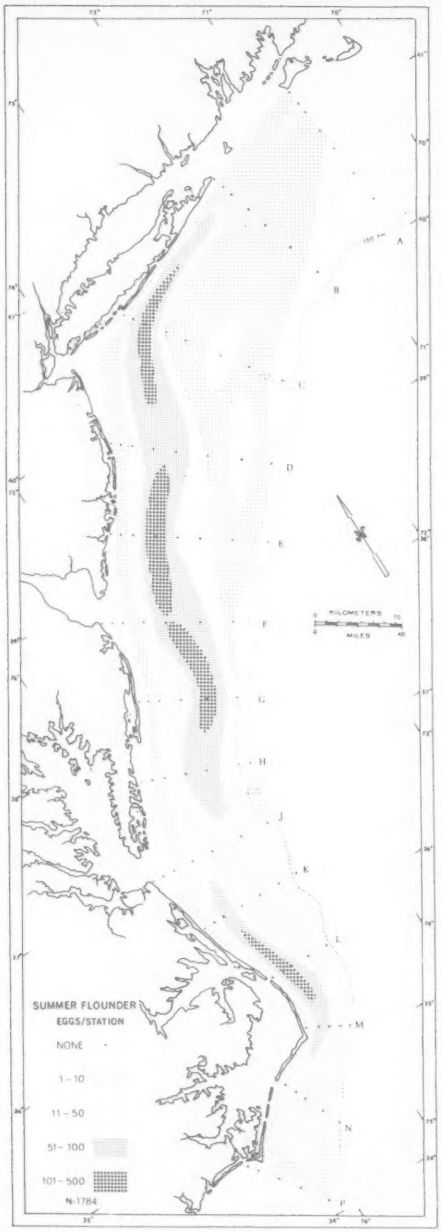

FIGURE 12.—Distribution and relative abundance (adjusted) of summer flounder eggs from 1965-66 plankton survey.

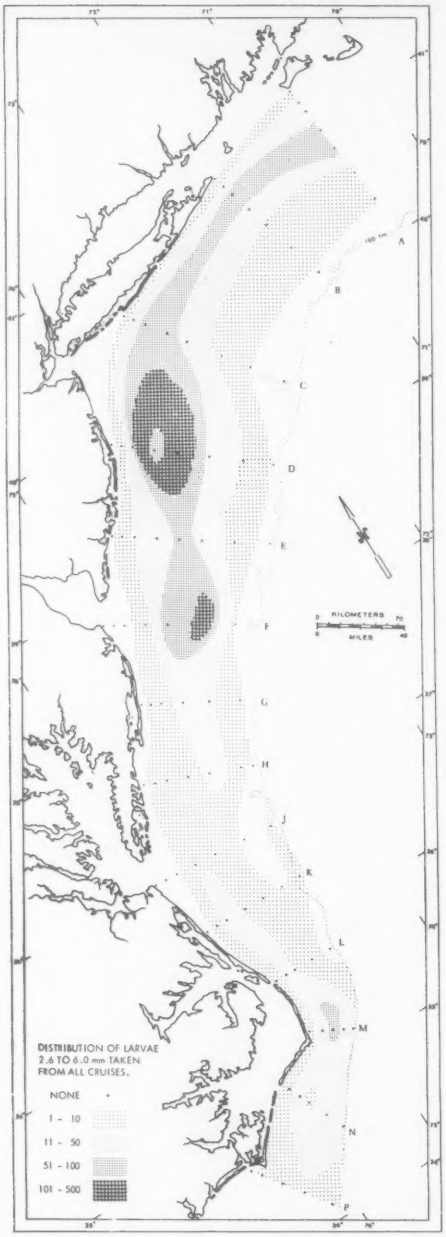

FIGURE 13.—Distribution and relative abundance (adjusted) of summer flounder larvae 2.6 to 6.0 mm from 1965-66 plankton survey.

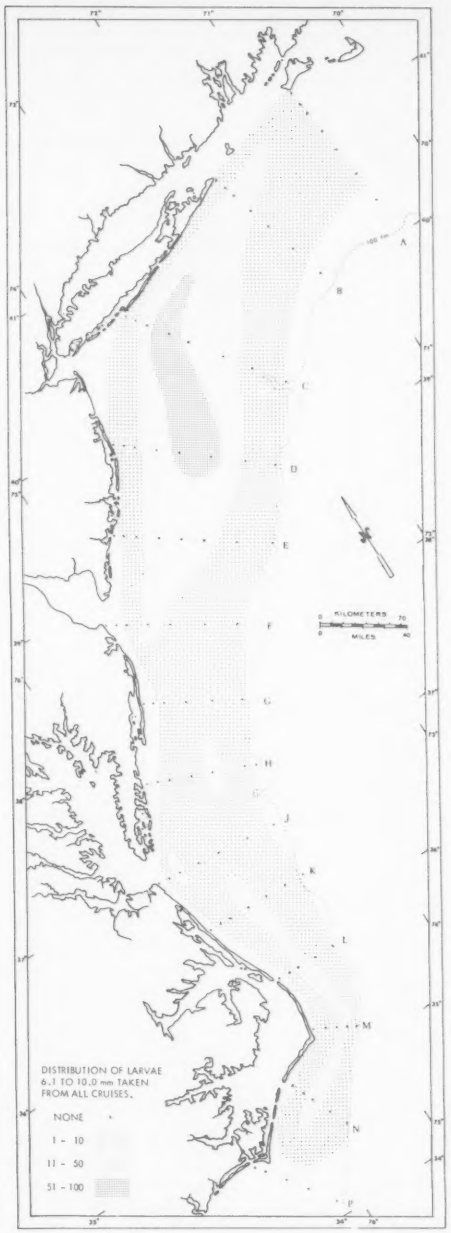

FIGURE 14.—Distribution and relative abundance (adjusted) of summer flounder larvae 6.1 to 10.0 mm from 1965-66 plankton survey.

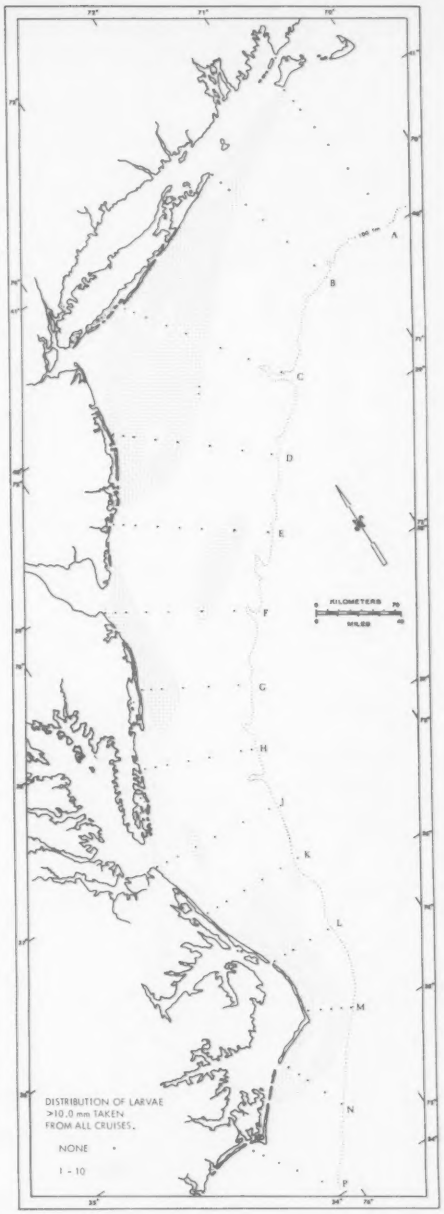

FIGURE 15.—Distribution and relative abundance (adjusted) of summer flounder larvae greater than 10.0 mm long from 1965-66 plankton survey.

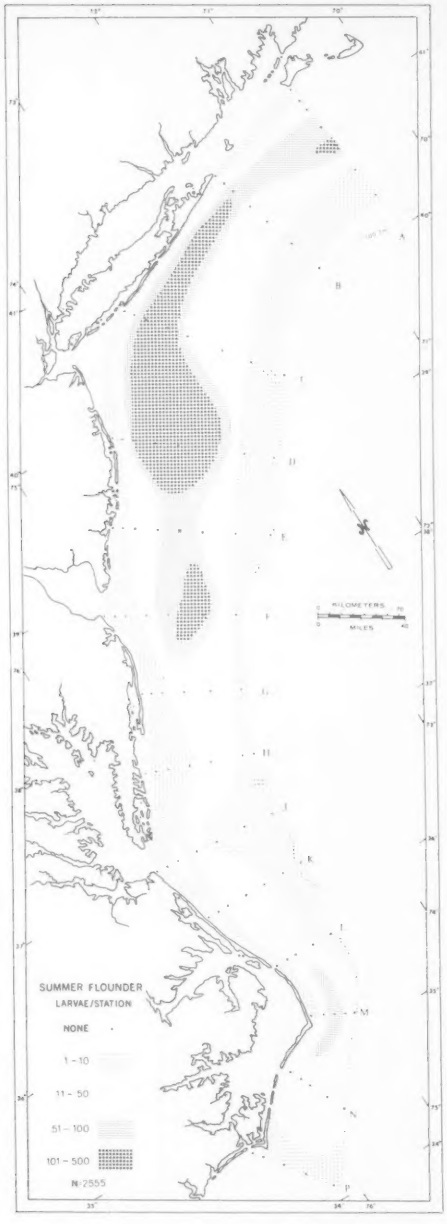

FIGURE 16.—Distribution and relative abundance (adjusted) of summer flounder larvae from 1965-66 plankton survey.

APPENDIX TABLE 1.—The length-frequency distribution of summer flounder larvae (to nearest 0.5 mm) taken on cruises from late summer to spring. Numbers are adjusted to standardize sampling effort of the two nets. Section I extended from Cape Cod to Cape Henlopen (Transects A to F); II from Cape Henlopen to Cape Hatteras (Transects G to M); and III from Cape Hatteras to Cape Lookout (Transects N and P). The survey began with the December 1965 cruise and ended with the November-December 1966 cruise.

Standard length (mm)	Cruise D-66-11 Sept. 1966				Cruise D-66-12 Oct. 1966				Cruise D-66-14 Nov.-Dec. 1966				Cruise D-65-4 Dec. 1965			
	Section				Section				Section				Section			
	I	II	III	Total	I	II	III	Total	I	II	III	Total	I	II	III	Total
2.6- 3.0	1			1	36			36	1	6	1	8		6	5	11
3.1- 3.5	5			5	148	3		151	12	17	3	32	5	30	18	53
3.6- 4.0	4			4	271	8		279	25	11	2	38	12	54	21	87
4.1- 4.5	3			3	182	10		192	42	9	1	52	19	47	13	79
4.6- 5.0	1			1	126	2		128	54	19	1	74	26	30	11	67
5.1- 5.5	1			1	112	1		113	46	9	1	56	48	23	6	77
5.6- 6.0					87			87	34	4		38	64	16	5	85
6.1- 6.5					69	1		70	20	10		30	60	30	1	91
6.6- 7.0					54			54	14	8	1	23	52	22	3	77
7.1- 7.5					18	1		19	17	8		25	34	26	2	62
7.6- 8.0					15			15	13	1		14	17	13	2	32
8.1- 8.5					7			7	17	1		18	18	11		29
8.6- 9.0					2			2	12			12	10	11		21
9.1- 9.5									9	1		10	6	7		13
9.6-10.0									2			2	2	6	1	9
10.1-10.5					1			1	7	1		8	4	3		7
10.6-11.0									6	5		11		5		5
11.1-11.5									3	2		5	2	2		4
11.6-12.0									1			1		1		1
12.1-12.5									1			1		2		2
12.6-13.0									1			1				
13.1-13.5													1	1		2
Total	15			15	1,128	26		1,154	337	112	10	459	380	346	88	814

Standard length (mm)	Cruise D-66-1 Jan.-Feb. 1966				Cruise D-66-3 Apr. 1966				Cruise D-66-5 May 1966				All cruises			
	Section				Section				Section				Section			
	I	II	III	Total	I	II	III	Total	I	II	III	Total	I	II	III	Total
2.6- 3.0													38	12	6	56
3.1- 3.5			4	4									170	50	25	245
3.6- 4.0			7	7			3	3					312	73	33	418
4.1- 4.5			5	5									246	66	19	331
4.6- 5.0			5	5			1	1					207	51	18	276
5.1- 5.5	1		3	4			1	1					208	33	11	252
5.6- 6.0							2	2					185	20	7	212
6.1- 6.5		1	2	3						1		1	149	43	3	195
6.6- 7.0			1	1			3	3					120	30	8	158
7.1- 7.5	1			1									70	35	2	107
7.6- 8.0		1		1			4	4					45	15	6	66
8.1- 8.5		2		2		1	6	7					42	15	6	63
8.6- 9.0	1	6	1	8		1	5	6		1		1	25	19	6	50
9.1- 9.5	1	4	1	6			5	5		2		2	16	14	6	36
9.6-10.0		1	1	2			2	2					4	7	4	15
10.1-10.5		3		3			3	3					12	7	3	22
10.6-11.0		1		1			1	1					6	11	1	18
11.1-11.5		1		1			1	1		2		2	5	7	1	13
11.6-12.0													1	1		2
12.1-12.5										1		1	1	3		4
12.6-13.0		1		1									1	1		2
13.1-13.5													1	1		2
Total	4	21	30	55		2	37	39		7		7	1,864	514	165	2,543

APPENDIX TABLE 2.—The relation of adjusted catch size of summer flounder eggs and larvae to mean temperature of water sampled by net no. 1 or no. 2. Only successful tows are included.

Mean temperature	Size of catch: 1-10 Eggs	1-10 Larvae	11-50 Eggs	11-50 Larvae	51-100 Eggs	51-100 Larvae	101-500 Eggs	101-500 Larvae	Total Eggs	Total Larvae
°C	*Number of tows*									
Less than 2.0		1								1
3.0- 3.9		4								4
4.0- 4.9		4								4
5.0- 5.9		1		1						2
7.0- 7.9		5								5
8.0- 8.9		11		4						15
9.0- 9.9	1	26		9		1			1	36
10.0-10.9		29		8						37
11.0-11.9	2	14		4		1			2	19
12.0-12.9	8	17	1	5		1			9	23
13.0-13.9	8	18	7	3	1				16	21
14.0-14.9	6	27	10	10	2	4	2		20	41
15.0-15.9	7	14	5	1	1	1			13	16
16.0-16.9	3	5	4	5					7	10
17.0-17.9	5	10	2	2	1	1	1	1	9	14
18.0-18.9	2	7	2	2					4	9
19.0-19.9	1	5			2				3	5
20.0-20.9	9	4	1	2					10	6
21.0-21.9	2	2							2	2
22.0-22.9	1	2							1	2
23.0-23.9		2								2
Total	55	208	32	56	7	9	3	1	97	274

APPENDIX TABLE 3.—The adjusted catch of summer flounder eggs and larvae, showing effort and relative densities by section and by transect. Section I extended from Cape Cod to Cape Henlopen; II from Cape Henlopen to Cape Hatteras; and III from Cape Hatteras to Cape Lookout. All stations sampled within a section where eggs or larvae occurred are included in density estimates, whether or not eggs or larvae were caught.

Section	Transect	Location	Eggs: Number of Standard tow	Eggs: Number of Eggs	Eggs: Catch per standard tow	Larvae: Number of Standard tow	Larvae: Number of Larvae	Larvae: Catch per standard tow
I	A	Martha's Vineyard, Mass.	21	21	1.0	23	224	9.7
	B	Eastern Long Island, N.Y.	21	17	0.8	28	186	6.8
	C	Western Long Island, N.Y.	24	179	7.5	40	388	9.7
	D	Barnegat Inlet, N.J.	24	187	7.8	40	637	15.9
	E	Great Egg Inlet, N.J.	16	241	15.1	32	210	6.6
	F	Cape Henlopen, Del.	14	167	11.9	27	253	9.4
Total			120	812	6.8	190	1,898	10.0
II	G	Assateague Island, Md.	18	192	10.7	30	72	2.4
	H	Eastern Shore, Va.	21	142	6.8	35	54	1.5
	J	Cape Henry, Va.	21	54	2.6	35	21	0.6
	K	Currituck Beach, N.C.	21	151	7.2	35	77	2.2
	X	Currituck Beach[1] to Oregon Inlet	4	0	0.0	4	54	13.5
	L	Oregon Inlet, N.C.	15	243	16.2	25	67	2.7
	M	Cape Hatteras, N.C.	15	126	8.4	25	151	6.0
Total			115	908	7.9	189	496	2.6
III	N	Ocracoke Inlet, N.C.	15	44	2.9	20	141	7.1
	P	Beaufort Inlet, N.C.	15	20	1.3	20	20	1.0
Total			30	64	2.1	40	161	4.0
Grand total			265	1,784	6.7	419	2,555	6.1

[1] Sampled only during December (1965) cruise.

EFFECTS OF TRANSPORTATION ON SURVIVAL AND HOMING OF SNAKE RIVER CHINOOK SALMON AND STEELHEAD TROUT

WESLEY J. EBEL, DONN L. PARK, AND RICHARD C. JOHNSEN[1]

ABSTRACT

The homing ability of adult fish that were captured during their seaward migration as juveniles and then transported downstream (from Ice Harbor Dam to Bonneville Dam) was not diminished. Data from returning adults indicated survival of adult fish that had been transported downstream as juveniles was higher than that of fish not transported. The percentage of increased survival ranged from 50 to 300% depending on the river environment during the time of transport. Information on the timing of the seaward migration and the extent of mixing of seaward runs of spring and summer chinook salmon, *Oncorhynchus tshawytscha*, was also obtained.

Losses to juvenile and adult Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, populations migrating in the Columbia and Snake Rivers have increased drastically in the last decade because of the effects of recently completed dams. The reservoirs formed by these dams have inundated some important spawning and rearing areas, have created new passage problems for both adult and juvenile migrants, and, in most cases, have significantly changed the aquatic environment to the detriment of salmonid fishes.

Gas bubble disease caused by high concentrations of dissolved nitrogen gas, resulting from the spilling of water at dams, has been pinpointed by the National Marine Fisheries Service (NMFS) (Ebel, 1969; Beiningen and Ebel, 1970; Ebel, 1971) as a major cause of salmon and steelhead trout mortalities. Nitrogen gas in the atmosphere is forced into solution as the water plunges into deep spill basins; the dissolved gas remains in solution in impounded sections of the river resulting in several hundred kilometers of water supersaturated with nitrogen gas through which fish must migrate. Another significant source of mortality can be due to passage of fish through turbines, particularly when indirect mortalities due to predation on fish emerging from turbines are included. These mortalities will persist even if nitrogen levels are reduced. Recent estimates (Raymond, 1970)[2] of losses to juvenile populations migrating downstream in the Snake and Columbia Rivers—that reflect losses from all sources, including nitrogen supersaturation—indicate that chinook salmon, *O. tshawytscha*, and steelhead trout from the upper Snake River drainage may be reduced to critically low numbers unless action is taken to reduce these losses.

NMFS has been conducting transportation experiments since 1965 to find ways of reducing these losses. Since 1968 we have been concentrating on an experiment where migrating juvenile salmon and trout—mostly spring and summer chinook salmon—are collected at Ice Harbor Dam and transported to two locations downstream. The experiment was designed to determine the effect of transportation on survival and homing.

Past information (Ellis and Noble, 1960; unpublished hatchery records of Washington,

[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2] Raymond, H. L. 1970. A summary of the 1969 and 1970 outmigration of juvenile chinook salmon and steelhead trout from the Snake River, Progress Report. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Biol. Lab., Seattle, Wash. Unpubl. manuscr.

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FISHERY BULLETIN: VOL. 71, NO. 2, 1973.

Oregon, and California) concerning the effect of transportation of hatchery stocks of juvenile chinook salmon, coho salmon, *O. kisutch*, and steelhead trout on homing indicates that the homing mechanism is disrupted by the transportation process. In these experiments, the majority of the adults returned to the location of release and not to the hatchery of origin.

We recognized this in pursuing our experiments but felt confident that different results would be obtained because we were dealing with juvenile fish, captured during their seaward migration, that had an entirely different life experience before being collected and transported. The wild stocks among our captured fish had lived for a year or more in their parent stream, were actively smolting at the time of capture, and had traversed several hundred kilometers of stream before they were transported. Captured hatchery stocks also were actively smolting at the time of capture and had traversed many kilometers before being collected. Transport experiments done by others have been conducted with hatchery stocks taken directly with no stream experience from hatchery ponds. Previous experiments (Groves, Collins, and Trefethen, 1968; Hasler and Wisby, 1951; and others) on mechanisms used by fish for homing suggest that the experience during the time that the juvenile salmon migrates seaward is important in enabling the fish to receive olfactory and visual cues necessary for homing as an adult. Since we were eliminating only a portion of the fish's migration route by transporting, we hypothesized that a fish would be successful in seeking its home stream and that survival to the spawning grounds as well as to the fishery would be increased.

The adult returns from releases of juvenile chinook salmon in 1968 and 1969 and of juvenile steelhead trout in 1969 and 1970 were obtained in 1970 and 1971. This report describes the results of the experiment based on information compiled to date. Adult returns from chinook salmon releases in 1969 and steelhead trout releases in 1970 were insufficient because 2- and 3-ocean returns are needed from data that will be obtained in 1971 and 1972 and, therefore, are not included in this report. A supplementary report will be made as additional information is received in future years.

METHODS

General Experimental Design

Three groups (one control and two transported) of migrating chinook salmon (spring- and summer-run populations) and steelhead trout were collected from gatewells at Ice Harbor Dam. Gatewell dip net hauls were mixed, then the test and control groups were selected randomly from the pooled dip net hauls. These were marked by removal of the adipose fin and with a thermal brand and a magnetized wire tag. The control, or non-transported, group was released about 15 km above Ice Harbor Dam. The transported groups were released 5 km downstream from John Day Dam on the Oregon side of the Columbia River and 1 km downstream from Bonneville on the Washington side of the river (Figure 1). A separate brand was assigned to each group and was changed weekly. A distinguishing color-coded wire tag was also assigned to the control and to the experimental groups. In 1968 one color-code was used on both transported groups. In 1969 and 1970 separate codes were assigned to each transported group.

All groups were hauled in a tank truck of 18,900-liter (5,000-gal) capacity that has been

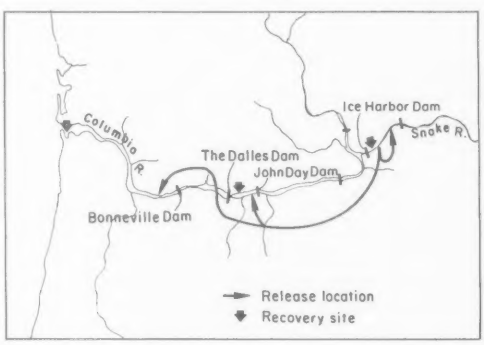

FIGURE 1.—Columbia and Snake Rivers, showing release and recovery sites of migrating chinook salmon and steelhead trout.

described by Ebel (1970). All releases were made at dusk. Records were kept of mortality during marking and at time of release.

This general procedure has been repeated during three downstream migrations—from 1968 through 1970. Each year our goal was to mark at least 50,000 fish per group but, because of low collection efficiency at the gatewells in 1969-70, this goal was reached only in 1968. In 1969 and 1970, steelhead trout were also included in the experiment.

Collection, Marking, and Hauling Procedures

In 1968-69 fish were obtained for the experiment by dipnetting them from gatewells (Bentley and Raymond, 1969). An orifice bypass system (Park and Farr, 1972) was completed in 1970 by the U.S. Army Corps of Engineers; we used this system as a source of fish in the spring of 1970. In 1969 and 1970, fish collected in the above manner were hauled by tank truck to a holding facility where they were held for about 24 hr before marking in denitrified water which had been pumped from the Snake River. Minor gas bubble disease subsided during the holding period, and presumably our holding procedure relieved some of the stress from this disease caused by the newly constructed dams upstream. In 1968, the disease was not a problem, and the fish were held and marked on the intake deck of the dam.

Fingerlings were brought into a marking building where they were anesthetized, examined for marks, and sorted by species. Marked fish were returned to the river; each of the remaining unmarked fish was cold-branded with liquid nitrogen (Mighell, 1969), the adipose fin was excised, and a magnetized wire tag was inserted in the snout (Jefferts, Bergman, and Fiscus, 1963). Before being placed into the transport truck, each fish went through a magnetic field (to magnetize the tag) and a detection coil; an improperly tagged fish was automatically rejected and returned to the marker for retagging. Steelhead trout and chinook salmon were kept in separate compartments in the truck whenever both species were hauled simultaneously. Load densities were governed by the size of a day's catch which never exceeded 10,000 fish. Thus loads were less than 60 g of fish per liter (½ lb. per gal) of water, which allowed a large margin of safety without loss of fish.

Water chemistry measurements were taken at the time of release for every load transported in 1968; in 1969 and 1970 only occasional water chemistry checks were made. Concentrations of ammonia, nitrogen, dissolved oxygen, carbon dioxide, pH, and total alkalinity were recorded.

Evaluation of Downstream Survival of Juveniles

Comparisons of the downstream survival of juvenile chinook salmon and steelhead trout released in the pool above Ice Harbor Dam and at John Day Dam were based on the proportions of these groups recovered from the gatewells by dipnetting at The Dalles Dam. Additional sampling with beach seines and purse seines was attempted in the Columbia River estuary. Samples from the estuary were to be used to evaluate survival to the sea.

Evaluation of Returning Adults

The effect of transportation on the survival and homing of adult fish was evaluated by comparing recoveries of transported and nontransported groups at various sites in the river system. These included returns to the sport, commercial, and Indian fisheries in the lower Columbia River; to Ice Harbor Dam on the lower Snake River; to Rapid River Hatchery (Idaho); and to the spawning grounds.

At Ice Harbor Dam about 80% of the run of adult fish ascends the south ladder enroute to the spawning grounds. We installed in this ladder a tag detector and adult separator device that intercepted tagged salmon and trout (Durkin, Ebel, and Smith, 1969) and diverted them into a holding pen (Figure 2). The tagged fish from our study were readily identified by the missing adipose fin. These were anesthetized and further examined for brands. If the brand was recognizable, the origin of the fish

could be determined without having to extract the magnetic tag from the snout. Fish with recognizable brands were then dart-tagged and released so that further information might be obtained upon recapture upstream or to identify the fish in case it fell back over the dam and ascended the ladder a second time. If a fish was known to be tagged but the brand was indistinguishable, it was tagged with a serially numbered dart and hauled to the Rapid River Hatchery where the fish was allowed to mature for spawn taking. The tag was then extracted after spawning, and the test or control group was determined from the color code.

The Columbia River gill net fishery below Bonneville Dam, the Indian fishery above the dam, and the sport fishery (primarily below the dam) were sampled throughout the spring chinook salmon run to provide information concerning the returns of our marked fish to the lower river. Closure of the summer fishery on chinook salmon prevented sampling of this segment of the run in the lower river. Steelhead trout were sampled in the sport and commercial fisheries of the lower river, but first year returns of fish from those marked in 1969 were insignificant.

Surveys of spawning grounds were conducted with the cooperation of the Washington Department of Fisheries, Fish Commission of Oregon, and the Idaho Fish and Game Department. Most of the surveys were in the Snake River drainage of Idaho, but hatcheries and spring and summer chinook spawning grounds in the upper Columbia River were also checked for strays.

RESULTS

Effect of Transport Mortality and Tag Loss on Analysis

Two factors that have bearing on the assessment of effects of transportation are transport mortality and tag loss.

Transport mortality is actually a combination mortality resulting from stresses of handling, marking, and hauling. During this study, mortality prior to hauling was less than 2% of the total number of fish collected. Of those marked and transported, however, about 5% died. This mortality was subtracted from the tallies of release group data in this report. Attempts were made to determine a delayed mortality after transport. These tests failed because holding conditions were unfavorable

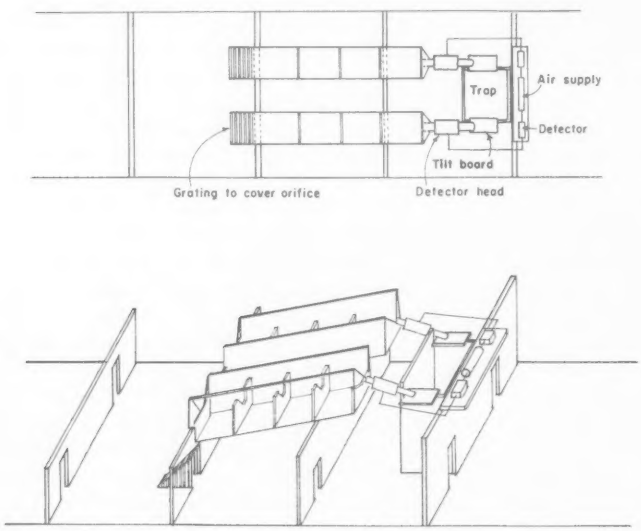

FIGURE 2.—Diagrammatic sketch of tag detector and separator device used for adult salmon and trout in south ladder of Ice Harbor Dam. Note trip board deflects tagged fish into trap.

and most fish probably died from factors other than stress from hauling.

One test, conducted with steelhead trout on 27-28 May, gives insight into the effect of transportation on smolts. Two groups of about 3,500 smolts each were released at the control group release site. Group I was treated similarly to that of our normal control group; i.e., the fish were hauled for about 1 hr before being released in the impoundment upstream from Ice Harbor Dam. Group II was treated in a like manner but was hauled for 7 hr before being released at the same site as group I. (This was approximately 2 hr longer than our typical hauls to date, but if transport tests in the future are made from points upstream, it is conceivable that 7 hr would be a minimum trip.) Upon examination of returns at Ice Harbor Dam, significantly ($\chi^2 = 4.300$; d.f. = 1) fewer fish returned from the long-haul group. More tests are required to establish an accurate posttransport mortality percentage.

Tag loss does not affect our information relating to effect of transportation on downstream survival. All data were adjusted for marking, handling, and transport mortality. Loss of tags is important when considering the results from returning adult fish. Insofar as affecting results of this study, apparent "tag loss" can occur in three ways: 1) Faulty machine operation—the smolt may never have been tagged; 2) the tag may be rejected at some time after being properly inserted in the snout; and 3) the fish can be tagged but the tag is not adequately magnetized. All have the same result—the returning fish cannot be detected. In 1968 our best information on initial tag loss was obtained from sampling at The Dalles Dam and from releases below Bonneville Dam. Although tag loss differed between release groups, overall weighted average tag loss on chinook salmon was 9.2%. Numbers of chinook salmon (transported and control) mentioned in this report have been adjusted on this basis. Tagging procedures were refined in 1969-70 so that tag loss is now less than 1% for both chinook salmon and steelhead trout.

Effect of Transportation on Downstream Survival of Juveniles

The best information concerning the effect of transportation on downstream survival of juveniles was obtained from catches in the gatewells of The Dalles Dam. The numbers of transported and nontransported (control) chinook salmon and steelhead trout that were marked and released are shown in Table 1. Recoveries at The Dalles Dam included only those fish transported to John Day Dam and the control releases above Ice Harbor Dam. Survival of the transported groups released at Bonneville Dam was estimated by recoveries in the estuary. Marked chinook salmon obtained from beach seine catches in the estuary were too limited (40 in 1968; none in 1969 and 1970) to reveal significant information. Table 2 compares recaptures of control and transported fish in 1968 that were released before and after heavy spilling began at The

TABLE 1.—Number of transported and nontransported (control) juvenile chinook salmon and steelhead trout that were marked and released, 1968-70 (figures adjusted for tag loss).

Release site and (in parentheses) experimental group of fish	1968	1969		1970	
	Chinook	Chinook	Steelhead	Chinook	Steelhead
Ice Harbor Dam (control)	80,335	24,217	25,313	8,624	18,347
John Day Dam (transported)	40,895	14,782	20,430	10,159	20,935
Bonneville Dam (transported)	42,420	13,529	—	10,173	31,282
Total	163,650	52,528	45,743	28,956	70,564

TABLE 2.—Releases and recaptures of transported and nontransported juvenile chinook salmon (transported fish were released below John Day Dam and nontransported fish were released above Ice Harbor Dam) that were recaptured at The Dalles Dam from releases before and after spilling began, 1968 (figures not adjusted for tag loss).

	Nontransported (control) fish					Transported fish				
Dates of release	Number released	Number recaptured	Dates of recapture	Percentage recapture	Recovery efficiency[1]	Number released	Number recaptured	Dates of recapture	Percentage recapture	Percentage increase in survival[2]
Before spill:										
4/2-4/5	425	13	4/22-5/8	—	—	0	0	—	0	—
	—	3	5/9-5/29	—	—	—	—	—	—	—
	—	16	—	3.76	5.74	—	—	—	—	—
4/8-4/12	4,128	175	4/22-5/22	—	—	1,352	67	4/16-5/16	—	—
	—	4	5/29-6/4	—	—	—	—	—	—	—
	—	179	—	4.34	4.56	—	—	—	4.96	—
4/15-4/19	7,843	1	4/26	—	—	7,305	416	4/22-5/25	—	—
	—	253	5/1-5/25	—	—	—	3	5/26-6/6	—	—
	—	17	5/26-6/14	—	—	—	0	—	—	—
	—	271	—	3.46	4.56	—	419	—	5.74	—
4/22-4/26	17,499	436	5/6-6/7	2.49	3.87	4,517	184	4/25-5/27	4.07	—
Totals	29,895	902	—	—	—	13,174	670	—	—	—
Cumulative average	—	—	—	3.02	5.09	—	—	—	5.09	69
After spill:										
4/28-5/4	15,711	241	5/9-5/30	—	—	9,222	347	5/1-5/25	—	—
	—	12	5/31-6/13	—	—	—	10	5/26-6/11	—	—
	—	253	—	1.61	3.88	—	357		3.87	—
5/5-5/11	21,964	190	5/16-6/11	0.86	3.88	8,730	340	5/8-6/12	3.89	—
5/12-5/17	11,371	48	5/22-6/12	0.42	2.64	6,446	212	5/16-6/14	3.29	—
5/18-5/22	5,200	—	—	—	—	2,791	27	5/22-5/30	—	—
	—	—	—	—	—	—	5	5/31-6/10	—	—
	—	7	5/27-6/6	0.13	1.15	—	32	—	1.15	—
5/23-6/7	2,290	0	—	0.00	0.00	3,601	4	6/5-6/12	0.11	—
Total	56,536	498	—	—	—	30,790	945	—	—	—
Cumulative average	—	—	—	—	0.88	—	—	—	3.07	249
Grand total	86,431	1,400	—	—	—	43,964	1,615	—	—	—
Cumulative average	—	—	—	1.62	3.67	—	—	—	3.67	127

[1] Recovery efficiency based on average percentage recapture of transported fish at The Dalles Dam for the recovery period shown. One hundred percent survival assumed between release site below John Day Dam and The Dalles Dam.
[2] Percentage increase in survival of transported groups equal to [(recovery efficiency) (100)/(% recapture of control)] - 100.

Dalles Dam. Recovery rates of survivors to The Dalles Dam varies tremendously depending on flow condition. Because the controls released at Ice Harbor Dam often took several days to reach The Dalles Dam, the recapture rate varied and was spread out over a longer period than the test groups. The recapture rate computed for the controls was therefore based on average recapture rate measured throughout the recovery period of the controls. As the table indicates, this rate was based on average percentage recovery rate of the test groups released during that period. It should be stressed that spilling also occurs at upstream dams once steady spilling begins at The Dalles. Before heavy spilling, the data indicate that survival of fish transported to John Day Dam was increased about 69%; the ratio of recapture of transport/control fish was 1.7:1. After heavy spilling, survival was increased by about 250% or 3.5:1.

In 1969 (Table 3), heavy spilling occurred

throughout the recapture period at The Dalles Dam. The overall average recovery of chinook salmon indicates that transportation increased survival by about 90%, or a ratio of about 1.9:1. Recapture data from steelhead trout indicated a 245% increased with a ratio of about 3.5:1. No downstream survival data were obtained in 1970.

Returns of Adult Spring and Summer Chinook Salmon to Ice Harbor Dam

Table 4 lists the number of adult salmon successfully detected, separated, and identified at the automatic separator in the south ladder at Ice Harbor Dam. It should be stressed that the observed return represents only a fraction of the total return of marked fish to Ice Harbor Dam. The observed tally is low for the following reasons: 1) Approximately 20% of the run at Ice Harbor passes up the right bank (North) fishway which did not have a tag detection device; 2) the tag detection system in the left bank (South) fishway was less than 100% efficient; 3) the system was operated less than full time during salmon runs; and 4) some tag losses had occurred between tagging and recovery.

The combined adult returns of spring and summer chinook salmon at Ice Harbor Dam to 31 July 1971 from juveniles marked in 1968 (Table 4) indicate that survival from releases at Bonneville Dam were significantly (χ^2 = 33.184; d.f. = 1) greater (2.0:1) than those from control releases at Ice Harbor. When these returns at Ice Harbor are divided into spring and summer seasonal races and

TABLE 3.—Releases and recaptures of transported and nontransported juvenile chinook salmon and steelhead trout transported fish were released below John Day Dam and nontransported fish were released above Ice Harbor Dam) that were recaptured at The Dalles Dam, 1969 (figures not adjusted for tag loss).

	Nontransported (control) fish					Transported fish				
Species and dates of release	Number released	Number recaptured	Dates of recapture	Percentage recapture	Recovery efficiency[1]	Number released	Number recaptured	Dates of recapture	Percentage recapture	Percentage increase in survival[2]
Chinook salmon:										
4/11-4/19	5,297	43	4/22-5/7	0.81	1.88	5,159	35	4/17-4/29	0.68	—
4/20-4/27	6,977	68	4/28-5/15	0.97	2.19	2,301	24	4/23-4/29	1.04	—
4/28-5/4	2,844	15	5/8-5/14	0.53	1.35	4,538	105	4/29-5/12	2.31	—
5/5-5/11	4,312	17	5/13-5/23	0.39	0.94	666	9	5/8-5/16	1.35	—
5/12-5/18	3,553	15	5/19-5/27	0.42	1.07	521	3	5/15-5/19	0.58	—
5/19-5/25	1,947	12	5/23-6/2	0.62	1.07	1,497	16	5/21-6/2	1.07	—
5/26-6/1	561	1	6/4	0.18	.80	878	7	6/3-6/5	0.80	—
Total	25,491	171	—	—	—	15,560	199	—	—	—
Cumulative average	—	—	—	0.67	1.28	—	—	—	1.28	91
Steelhead trout:										
4/11-4/19	1,184	8	4/23-5/2	0.68	—	0	0	—	—	—
4/20-4/27	3,812	11	4/28-5/8	0.29	1.59	0	0	—	—	—
4/28-5/4	2,379	14	5/8-5/21	0.59	1.36	4,207	67	5/2-5/16	1.59	—
5/5-5/11	6,036	27	5/9-5/23	0.45	1.46	4,635	63	5/7-5/20	1.36	—
5/12-5/18	7,497	25	5/16-6/2	0.33	1.24	6,785	106	5/15-5/27	1.56	—
5/19-5/25	4,421	14	5/23-6/9	0.32	0.74	3,441	32	5/21-6/4	0.93	—
5/26-6/1	1,316	1	6/4	0.08	—	2,437	14	5/28-6/4	0.57	—
Total	26,645	100	—	—	—	21,505	282	—	—	—
Cumulative average	—	—	—	0.38	1.31	—	—	—	1.31	245

[1] Recovery efficiency based on average percentage recapture of transported fish at The Dalles Dam for the recovery period shown. One hundred percent survival assumed between release site below John Day Dam and The Dalles Dam.
[2] Percentage increase in survival of transported groups equal to [(recovery efficiency) (100)/(% recapture of control)] - 100.

TABLE 4.—Percentage of transported and nontransported (control) juvenile chinook salmon (released in 1968) that were recaptured as adults at Ice Harbor Dam, 1 April through 30 September 1970 and 1971.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults	Percentage return as adults	
			Observed	Estimated[2]
Ice Harbor Dam (control)	80,335	117	0.14	4.3
John Day Dam (transported)	40,895	64	0.16	4.7
Bonneville Dam (transported)	42,420	128	0.30	9.0
Total	163,650	309	0.19 Ave.	5.6

[1] Adjusted for initial tag loss.
[2] Based on a comparison of the known recovery of fish with magnetized wire tags at Ice Harbor Dam and the subsequent recovery of these and other marked fish at a hatchery upstream from Ice Harbor. Returning fish identified at the dam were marked with dart tags and released to continue their migration upstream. Numbers of dart-tagged fish arriving at Rapid River Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Ice Harbor Dam.

compared (Table 5), benefits from transportation are defined by time. Returns of spring chinook salmon are in a ratio of 1.8:1 (transport/control) and summer chinook salmon in a ratio of 2.8:1.

TABLE 5.—A comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish (released at Bonneville and John Day Dams) that were recaptured as adults at Ice Harbor Dam in 1970 and 1971.

Release site (of juveniles) and seasonal race of salmon[1]	No. of salmon recaptured[2] as adults at Ice Harbor Dam		Transport/control ratio of fish
	Transported	Nontransported (control)	
Below Bonneville Dam:			
Spring chinook salmon	161	88	1.8:1
Summer chinook salmon	82	29	2.8:1
Below John Day Dam:			
Spring chinook salmon	92	88	1.05:1
Summer chinook salmon	36	29	1.24:1

[1] Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn. We classified adult salmon captured at Ice Harbor Dam prior to 2 June as spring chinook and those taken from 2 June through 31 July as summer chinook.
[2] Numbers recaptured adjusted in relation to numbers released (Table 1).

Combined adult returns from the John Day release were only slightly more than returns from the controls. Although the poorer returns from releases at John Day are unexplained at this time, it is possible that the stress on the fish from having to pass two dams (The Dalles and Bonneville) plus the stress of being hauled may have eliminated any benefit from transport prior to spilling. If returns from this release are again separated into seasonal races, however, the ratio of transport to control of the summer chinook salmon is about 1.3:1.

A comparison of adult returns to Ice Harbor Dam from the Bonneville releases with estimates of juvenile survival at The Dalles Dam indicates a correspondence. Prior to heavy spilling when the majority of the spring chinook salmon migrated, the recovery ratio of juveniles released before spilling began was 1.7:1 (transport/controls); adult return ratio at Ice Harbor was 1.8:1 for spring chinook salmon. After heavy spilling when the majority of the summer chinook salmon migrated, the recovery ratio of juveniles released then was 3.5:1; adult return ratio of summer chinook salmon was 2.8:1.

Logically, the adult return ratios indicated from those transported to Bonneville Dam should show more benefit from transport than the juvenile ratios showed at The Dalles Dam because the controls still had to pass two dams, The Dalles and Bonneville, before reaching the ocean. This is not the case; only the spring chinook salmon show a greater ratio; the summer chinook salmon transport/control return ratios for juvenile migrants were higher than the adult ratios established at Ice Harbor Dam.

Returns of Adult Steelhead Trout to Ice Harbor Dam

The first adults returning from control releases and those transported to John Day in 1969 appeared at Ice Harbor Dam in the fall of 1970; in the following year, a second group of older fish returned. We detected 143 steelhead trout with coded wire tags and identified them in the trap at Ice Harbor Dam in 1970 and 1971. Of these, 46 were from the control

release, 97 from the transported release—a ratio of 2.1:1 of transport/control. This return ratio is higher than that shown for the returns of summer chinook salmon transported and released at John Day. Although the juvenile fish migrated downstream in different years (1968 for chinook salmon; 1969 for steelhead trout), environmental conditions were similar. During both years, heavy spilling prevailed at the time of release and concentrations of dissolved nitrogen gas were very high.

If gas bubble disease caused by supersaturation of nitrogen was the main factor determining survival of these groups, susceptibility of the salmon and trout to lethal levels of nitrogen gas in the river must have been similar or the ratios of returning adults would not have been similar. This, of course, is merely a hypothesis; several other factors which cause change in survival could also have been responsible for the similarity of the ratios.

This return ratio also indicates that the ability of steelhead trout to return or "home" to Ice Harbor Dam was not appreciably affected by transporting the seaward migrants around a portion of their downstream route.

Recovery of Marked Chinook Salmon in Commercial and Sport Fisheries

Returns to the commercial and sport fisheries in the lower Columbia River (Table 6) are based on the spring fishery and indicate a definite benefit from transportation. The return ratio of transported fish (John Day-Bonneville releases combined) to control fish was 1.4:1. The marked increase in the transport/control ratio for summer-run adults taken at Ice Harbor Dam is not reflected in the commercial fishery because of the closure on summer-run chinook salmon.

It was not possible to distinguish between returns to the fishery from releases at Bonneville and John Day because of the loss of the identifying brands. Brands which would have enabled identification by release site were obliterated by gill-net abrasion. Transported and control groups could be distinguished by magnetic tags, but only two codes were used—one for the controls and one for the transported fish. However, if the percentage of adult returns obtained at Ice Harbor—where brands of fish returning from releases at Bonneville and John Day were visible—is applied to the total transport returns obtained in the commercial fishery, the ratio of transport/control becomes 1.7:1 for fish transported to Bonneville Dam.

TABLE 6.—A comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish that were recaptured as adults by commercial and sport fisheries in the lower Columbia River, 23 February through 11 August 1970 and 1971.

Location of fisheries	No. of salmon recaptured as adults	
	Transported	Nontransported (control)
Upstream from Bonneville Dam (Indian fishery)	37	16
Downstream from Bonneville Dam	95	78
Total	132	94

Returns of Adults to Spawning Grounds

Spring and Summer Chinook Salmon

Spawning ground surveys (Figure 3) and examination of tagged adult fish at Rapid River Hatchery near Riggins, Idaho, provided further information concerning the ratios of transport/control spring and summer chinook salmon at their "home" destination. During the study, 65 tagged fish were recovered from Rapid River Hatchery; an additional 29 were from sport fishermen and spawning ground surveys. Of these fish, 52 were from the transported groups and 42 from the control group. By adjusting for the ratio of John Day to Bonneville returns, we estimated that 36 of the 52 transported fish were from the group released at Bonneville Dam. The ratio, then, of transport/control fish for the group released at Bonneville becomes 1.7:1 when computed on the basis of the number of juveniles released per group. This is nearly identical to

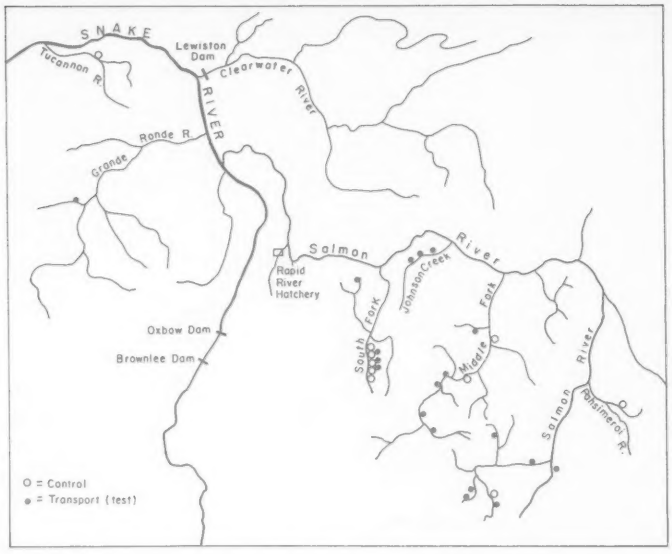

FIGURE 3.—Location of tagged adult chinook salmon returns from spawning ground surveys and returns of tags from sport fishermen in the Snake River drainage.

the ratio at Ice Harbor Dam for the Bonneville release, indicating no straying or loss of homing between Ice Harbor Dam and the spawning grounds.

The chinook salmon spawning grounds of the Okanogan and Methow Rivers and the hatcheries on the Columbia River above and below the mouth of the Snake River were checked for returning tagged adults, but no tagged fish were found. Thus, if straying to these areas did occur, it was too small to detect.

Steelhead Trout

Information on the return of adult steelhead trout to their spawning ground is based solely on recoveries of dart tags by sport fishermen. To date (January 1972) only nine tags have been recovered—two from the control group and seven from the transported group.

Timing of Seaward Migration of Juvenile Fish in Relation to Adult Returns

Spring and Summer Chinook Salmon

During marking of juveniles in 1968, a distinctive brand was used each week for the transport and control groups. These identifying brands provided a means of comparing the timing of the downstream migration of the juvenile fish with the timing of the upstream (spawning) migration of the adult fish. Only a small number (57) of adult returns could be used for this comparison because the brand on the adult fish had to be absolutely legible to determine the time of downstream migration. Returns from the control group could not be used because poor environmental conditions caused by supersaturation of dissolved nitrogen gas apparently wiped out whole groups of juvenile fish that were released during the highest nitrogen concentration. For example, over 37,000 fish were marked for the control group and released between 5 May and 27 May; only 1 adult fish was recovered from those marked during that period.

Adult returns of juveniles marked and transported between 12 April and 13 May indicate that the juvenile population at that time is mixed, with juvenile summer and spring chinook salmon evenly dispersed. Of 37 adult returns from groups marked and transported during this period, 20 were spring chinook and 17 were summer chinook salmon.

Adult returns (14 of 20) from those marked and transported after 13 May indicated that about 70% of the juveniles migrating seaward after that date were summer chinook salmon. All returns (11) from those marked after 19 May were summer chinook salmon—again indicating that the latest juvenile outmigrants are from summer chinook salmon populations.

This, in part, explains why the benefit from transport (2.8:1 ratio of transport/control fish) was so much higher for summer chinook salmon than for spring chinook salmon. After heavy spilling at dams, from early May on, a higher proportion of the juvenile population consisted of summer chinook salmon. The obvious implication is that the control groups released from this time on were largely wiped out by gas bubble disease, caused by high concentrations of nitrogen gas from the heavy spillway discharges.

Steelhead Trout

Juvenile steelhead trout were transported from 28 April to 1 June 1969, each group being marked with a distinctive weekly brand; 90% of those that returned as adults in 1970 arrived at Ice Harbor between 24 September and 14 October. There was no particular relation between time of seaward migration and time of return. Adult returns from juveniles marked between 28 April and 1 June were equally distributed throughout the return period, 24 September-14 October.

We examined scales to determine whether the adults were predominantly 1- or 2-year freshwater smolts at the time of their downstream migration. All adults had lived 2 years or more in fresh water. Only 19 scale samples, however, had legible freshwater annuli. The size of these fish was of interest. After spending only 1 year in the ocean, they averaged 61 cm and 2.6 kg. No significant difference was found between size of control fish and transported fish.

Retention of Cold Brand and Magnetic Tag

We were particularly interested in determining the percentage of brand retention on adult fish that had been cold branded as juveniles during the course of this study. Both cold (Mighell, 1969) and hot (Groves and Novotny, 1965) brands have been used successfully as short-term marks on chinook salmon and steelhead trout; up to the time of this study, however, no information was available concerning the retention of the brand to adulthood by chinook salmon and steelhead trout.

Clifford Long (National Marine Fisheries Service, Pasco, Wash., pers. comm.) determined that the brand was retained by 70% of the jack coho salmon marked for his studies; the Fish Commission of Oregon had similar results with coho salmon they had branded (Groves and Jones, 1969). Although we attempted to duplicate the techniques used by the above authors, the salmon and trout that we branded did not retain brands as well as the retention reported for coho salmon. Forty percent of our brands were not detectable on the spring and summer chinook salmon when they returned as adults (Table 7). The brand was legible (Figure 4) on 38% but only partially legible on 22%. Of the steelhead trout brands, 64% were legible, 24% illegible, and 12% partially legible. The size and physiological condition of the fish at the time of marking may have affected brand retention. The chinook salmon and steelhead trout we marked were smolting. Size range of the chinook salmon was 80-140 mm and of the steelhead trout, 160-250 mm.

Average overall tag loss for all groups was determined by comparing returns to Rapid River Hatchery of: 1) adults with adipose fin clips and wire nose tags with 2) adults with adipose fin clips only.

Approximately 27% of the juvenile chinook

TABLE 7.—Quality of marks ("cold" brands) on adult chinook salmon and steelhead trout that had been branded as juveniles during their downstream migration.

Species	Total no. of fish examined	Fish with legible marks		Fish with partially legible marks		Fish without readily identifiable marks	
		No.	%	No.	%	No.	%
Chinook	212	80	38	46	22	86	40
Steelhead	115	74	64	13	12	28	24

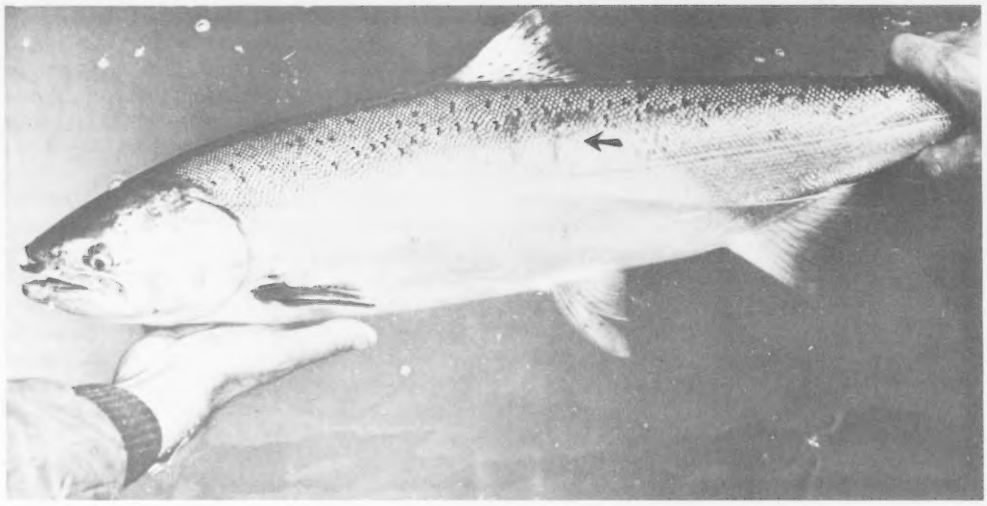

FIGURE 4.—Spring chinook salmon with legible brand (arrow) captured at Ice Harbor Dam, spring 1970.

salmon we tagged lost their tags between the time they were released as juveniles and returned as adults. The weighted average initial tag loss of all groups measured after release of juveniles in the river was 9.2%. This was computed by checking recaptured juveniles with brands and clips at The Dalles Dam and by checking samples of fish released below Bonneville Dam. Obviously an additional 18% tag loss occurred sometime after the 9.2% figure was established. This is much higher than the loss (0.31%) determined by Bergman et al. (1968). There are several possible explanations for this high loss: 1) The population we marked had a much wider size range than the hatchery stock Bergman et al. used, and this could have resulted in poor placement of the tag in those fish that were either too large or small for the tagging machine; 2) our fish taggers were inexperienced in operation of the machine; or 3) the Snake River has a high incidence of pathogens which could cause infection of the tag wound, resulting in rejection of the tag at a later date.

A combination of the above factors probably accounts for the high tag loss in our initial experiments. We believe that continued training and experience of the tagging personnel will result in a major reduction of tag loss in the future. For example, initial tag loss in 1969 was reduced to 5% and in 1970, to less than 1%. Although the loss was high in 1968, it could be compensated for mathematically. The basic information we needed from the data was not affected.

DISCUSSION

All comparisons between the returns of transported and control groups of spring chinook salmon indicate that survival was definitely increased by transporting juvenile fish to a release site downstream from Bonneville Dam. The ratios varied from 1.7:1 in the commercial fishery to 1.8:1 at Ice Harbor Dam. Comparison between the control and transported groups of summer chinook salmon can be made only at Ice Harbor Dam. No returns were obtainable in the sport and commercial fishery because direct fisheries on these fish have been restricted in recent years due to decline in the size of run; only nine returns were obtained on the spawning grounds. The return ratio (2.8:1) at Ice Harbor Dam, however, clearly indicates a definite increase in survival of transported summer chinook salmon.

These ratios also provide information on the effect of transportation on homing and

straying. A steadily decreasing ratio of transport/control numbers from the commercial fishery below Bonneville to the spawning grounds would indicate a loss of homing ability, straying, or differential mortality between groups. The ratios established for the test group released at Bonneville were 1.7:1, 1.8:1, and 1.7:1 for the commercial fishery, Ice Harbor Dam, and the spawning grounds, respectively. This indicates that no loss of the transport group occurred between Astoria (Oreg.), Ice Harbor Dam, and the spawning grounds. The same relation between ratios exists if the returns from releases at John Day and Bonneville Dam are combined; i.e., no loss of the transport groups occurred between Astoria and Ice Harbor Dam. If the homing ability of some fish was lost, any loss of fish due to straying was compensated for by an increase in survival and return of transported fish to both the fishery and spawning grounds.

Certain assumptions have been made to determine, and then compare, ratios and percentage returns of fish from transported and control groups. These are:

1. No differential mortality occurred between control and transported fish as they moved upstream from the mouth of the river to the spawning grounds; i.e., adult return ratios of the numbers of transport/control fish in the commercial and sport fishery in the lower river can be directly compared with the observed ratios at Ice Harbor Dam and the spawning grounds to provide an indicator of the effect of transportation on homing or straying.

2. The adult return ratio of John Day/Bonneville transported fish remained constant after these fish entered the Columbia River. We must assume this when the ratio is used to determine the actual number of fish of the John Day and Bonneville groups in returns to the commercial fishery and to spawning grounds (where the brands were not visible) and when it is then necessary to rely on the single tag code to calculate return data for the two transported groups.

3. Native and hatchery stocks in our control and transported groups were recovered at the same rate by the detector and separator at Ice Harbor Dam. This assumption is necessary inasmuch as the estimated percentage return of all adults to Ice Harbor (Table 4) was based solely on the ratio of observed recoveries of a hatchery stock (Rapid River stock) at Ice Harbor and those subsequently recovered at the hatchery. Recoveries of native fish on the spawning grounds from fish identified at Ice Harbor were insufficient for use in this application.

4. Rate of maturity and timing of migration is the same for transport and controls. Since ocean and river fishing rates are not the same on fish maturing early and returning early as they are on fish maturing late and returning late, this assumption is required.

The most significant result of this study is that the ability of the chinook salmon and steelhead trout to return to Ice Harbor Dam was not destroyed or even seriously affected by transporting seaward migrants around a major part of their downstream route. Overall returns from transported groups, except those from the early releases at John Day Dam, were significantly greater than those from the control group. These results are radically different from any achieved to date in other experiments (Ellis and Noble, 1960; unpublished hatchery records of Washington, Oregon, and California) where hatchery stocks exclusively had been transported. We are therefore convinced that our original hypothesis is acceptable—namely, that a fish's experience from the period beginning with smolting to the time the fish is collected for transport is critical. Our understanding of the mechanisms of homing is still limited, however, and much more must be learned to fully understand what the critical factors are in determining what is needed to provide anadromous salmon and trout with homing cues. Experiments to pinpoint the critical requirements for imprinting are needed. If these factors can be determined, it might be possible to provide the necessary experience in a hatchery prior to transport which would enable transport of fish directly from the rearing areas to locations downstream and thus eliminate much of the usual downstream mortality and still achieve satisfactory

returns to the hatchery concomitant with greater returns to the fishery.

The information we have to date is sufficient to consider the feasibility of a major collection and transportation system on the Snake and Columbia Rivers. An evaluation of a prototype system was initiated at Little Goose Dam on the Snake River in the spring of 1971. The results of that study, we believe, should lead to a determination of whether collection and transportation of juvenile salmon and trout is, indeed, feasible and can provide substantial protection for runs from upriver areas.

CONCLUSION

1. The homing of adult fish that were captured during their seaward migration as juveniles and then transported (from upstream of Ice Harbor Dam to below Bonneville Dam) downstream was not reduced by the transportation operation. A comparison of the transport/control ratios of returning adults in the lower river with those at Ice Harbor Dam and the spawning grounds indicated that no loss to the transport groups occurred between the estuary, Ice Harbor Dam, and the spawning ground. Straying of either the transported or control groups was not indicated in surveys of hatcheries and spawning grounds.

2. Data from adult returns indicated that transportation of naturally migrating juvenile spring- and summer-run chinook salmon and of steelhead trout from upstream of Ice Harbor Dam to below Bonneville Dam definitely increased returns (50-300%) to the fishery and to Ice Harbor Dam, depending on the river environment during the time of transport.

3. Transportation of juvenile spring chinook salmon to the release site below John Day Dam did not increase their survival (as evidenced by adult returns) during the period before the dams began heavy spilling but did increase survival about 15% after heavy spilling began.

4. The juvenile population of chinook salmon migrating seaward past Ice Harbor Dam from 12 April to 13 May in 1968 was of mixed seasonal races—with juvenile summer and spring chinook salmon mixed and evenly dispersed throughout the period. After 13 May, about 70% of the juvenile chinook salmon were summer-run fish.

5. Quality of brands on adult fish that had been marked as juveniles (using tools that were chilled with liquid nitrogen) varied between species—38% of the marks on spring and summer chinook salmon were legible compared with 64% on steelhead trout.

6. Relative effects of transport over controls is demonstrated, but effects of handling on both groups has not been evaluated. Thus, the survival of transported fish needs to be compared with survival of undisturbed migrants and is currently being studied.

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LITERATURE CITED

BEININGEN, K. T., AND W. J. EBEL.
1970. Effect of John Day Dam on dissolved nitrogen concentrations and salmon in the Columbia River, 1968. Trans. Am. Fish. Soc. 99:664-671.

BENTLEY, W. W., AND H. L. RAYMOND.
1969. Passage of juvenile fish through orifices in gatewells of turbine intakes at McNary Dam. Trans. Am. Fish. Soc. 98:723-727.

BERGMAN, P. K., K. B. JEFFERTS, H. F. FISCUS, AND R. C. HAGER.
1968. A preliminary evaluation of an implanted, coded wire fish tag. Wash. Dep. Fish., Fish. Res. Pap. 3(1):63-84.

DURKIN, J. T., W. J. EBEL, AND J. R. SMITH.
1969. A device to detect magnetized wire tags in migrating adult coho salmon. J. Fish. Res. Board Can. 26:3083-3088.

EBEL, W. J.
1969. Supersaturation of nitrogen in the Columbia River and its effect on salmon and steelhead trout. U.S. Fish Wildl. Serv., Fish. Bull. 68:1-11.

1970. Effect of release location on survival of juvenile fall chinook salmon, *Oncorhynchus tshawytscha*. Trans. Am. Fish. Soc. 99:672-676.

1971. Dissolved nitrogen concentrations in the Columbia and Snake Rivers in 1970 and their effect on chinook salmon and steelhead trout. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-646, 7 p.

ELLIS, C. H., AND R. E. NOBLE.
1960. Barging and hauling experiments with fall chinook salmon on the Klickitat River to test effects on survivals. Wash. Dep. Fish., 70th Annu. Rep.:57-71.

GROVES, A. B., G. B. COLLINS, AND P. S. TREFETHEN.
1968. Roles of olfaction and vision in choice of spawning site by homing adult chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 25:867-876.

GROVES, A. B., AND I. W. JONES.
1969. Permanent thermal branding of coho salmon, *Oncorhynchus kisutch*. Trans. Am. Fish. Soc. 98:334-335.

GROVES, A. B., AND A. J. NOVOTNY.
1965. A thermal-marking technique for juvenile salmonids. Trans. Am. Fish. Soc. 94:386-389.

HASLER, A. D., AND W. J. WISBY.
1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Am. Nat. 85:223-238.

JEFFERTS, K. B., P. K. BERGMAN, AND H. F. FISCUS.
1963. A coded wire identification system for macro-organisms. Nature (Lond.) 198:460-462.

MIGHELL, J. L.
1969. Rapid cold-branding of salmon and trout with liquid nitrogen. J. Fish. Res. Board Can. 26:2765-2769.

PARK, D. L., AND W. E. FARR.
1972. Collection of juvenile salmon and steelhead trout passing through orifices in gatewells of turbine intakes at Ice Harbor Dam. Trans. Am. Fish. Soc. 101:381-384.

DIGESTIVE SYSTEM AND FEEDING HABITS OF THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*, A STOMACHLESS FISH[1,2]

LABBISH NING CHAO[3]

ABSTRACT

The cunner, *Tautogolabrus adspersus*, completely lacks a morphologically or physiologically distinct stomach. The alimentary tract consists of the pharynx followed by a short esophagus with an esophageal-intestinal valve at the junction of esophagus and intestine. The intestine has three limbs and an S-loop. The intestinal bulb where the bile duct enters is present at the anterior end of the first limb. The border between the posterior end of S-loop and the rectum is marked by the intestinal-rectal valve. Histological and histochemical observations indicate that the rodlet cells, wandering cells, longitudinal muscle layers, and the rectal valve differ in minor ways from those of other stomachless fishes. Different forms of rodlet cells are found in the bile duct. An alkaline condition (pH values between 7.0 and 8.5) prevails throughout the alimentary tract. Alkaline phosphatase reaction was demonstrated only when food was present in the gut. Cunner are carnivorous, and the feeding habits change with growth. Juveniles feed mainly on planktonic crustacea and adults on sessile animals (mussels and barnacles). The time between ingestion and defecation of mussels (Mytilidae) by cunner is 10 to 14 hr. Intact mussels can pass through the alimentary tract of the fish undamaged and alive.

The most abundant labrid of the New England region, the cunner, *Tautogolabrus adspersus* (Walbaum), lacks a stomach. The absence of a stomach is here defined as the lack of an expansion of the alimentary tract between the end of the esophagus and the entrance of the bile duct into the intestine (Figure 1). The mucosa of this region lacks gastric epithelium and gastric glands. The alimentary tract is alkaline and lacks peptic digestion. Lack of a stomach appears to be a phylogenetic characteristic of the family rather than an adaptive one associated with feeding in this particular species.

The absence of a morphological stomach in teleostean fishes has been recorded in various species of several families, i.e., Atherinidae, Blenniidae, Callionymidae, Cobitidae, Cyprinidae, Cyprinodontidae, Gobiesocidae, Gobiidae, Labridae, Mugilidae, Poeciliidae, Scaridae, and Syngnathidae. These families have different feeding habits as noted by Ishida (1936), Barrington (1942), Suyehiro (1942), and Al-Hussaini (1947b) and are not closely related phylogenetically. Al-Hussaini (1949a) also recorded different feeding habits among three stomachless species of the family Cyprinidae: *Cyprinus carpio*, *Rutilus rutilus*, and *Gobio gobio*; they are herbivorous, omnivorous, and carnivorous, respectively. Physiological lack of stomach has been noted in various fishes: *Fundulus heteroclitus* by Babkin and Bowie

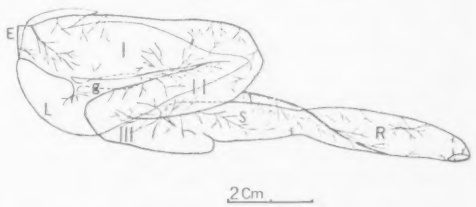

FIGURE 1.—Lateral view of the alimentary tract of a 280-mm SL cunner. E, esophagus; g, gallbladder; I, II, III, sections of intestine; S, S-loop of intestine; L, liver; R, rectum.

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[2] A portion of a thesis submitted to the Department of Biology, Northeastern University, Boston, Mass., in partial fulfillment of the requirements for the degree of Master of Science in Biology, January 1972.

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(1928); Cyprinidae by Szarski (1956); *Spheroides niphobles* by Ishida (1936); Scaridae and Labridae by Gohar and Latif (1959). Both morphological and physiological characters of the stomachless fishes appear to be characteristic of the Labridae.

The morpholoy and histology of the entire alimentary tract in the cunner were described from the protrusible lip to the anal papillae. A histochemical study was made on the gut, i.e., the postpharyngeal portion of the alimentary tract. Also, feeding habits and habitat, gut contents, and the movement and digestion of food were investigated.

MATERIALS AND METHODS

The fish were collected at East Point, Nahant, Mass., from May to September 1970 and 1971. Larger specimens, over 100 mm SL (standard length), were taken by hook and line fishing along the shore, and smaller ones in plankton hauls, by bottom dredging, hand netting, and rotenone poisoning in tide pools. Some specimens were maintained in constant running seawater aquaria and fed with mussels (Mytilidae).

Histological and histochemical studies were made after starvation (7-10 days) and after feeding. Specimens less than 40 mm SL were killed in 10% Formalin,[4] larger ones by severing the spinal cord and by intracoelomic injection of Dilantin (sodium diphenylhydantoin, USP) anesthetic (0.1 ml/10 g body weight). Tissues were fixed with absolute acetone, Baker's Formalin, Bouin's (also with seawater), Helly's, Hollande-Bouin's or Zenker's fixatives in order to demonstrate specific cell types. After fixation, dehydration was done in two ways: the standard method of ethyl alcohol or from water to Cellosolve (2-ethoxyethanol). Infiltration and embedding were carried out using Steedman polyester wax (1960); serial sections were cut at 1 to 8 μ. A variety of routine histological and histochemical stains were used, including hematoxylins (Ehrlich's, Galigher's, Heidenhain's Iron Alum, Groat's) counterstained with eosin or fast green, Giemsa (Mallory, 1944, in Humason, 1967), Gomori's trichrome (1950, in Humason 1967), Heidenhain's azan (1938, in Humason, 1967), Masson's trichrome mixture (Gurr, 1956, in Humason, 1967). Histochemical methods included: alcian blue (Steedman, 1950; modified by Mowry, 1956, 1963, in Humason, 1967), periodic acid Shiff's technique (McManns and Mowry, 1960, in Humason, 1967), toluidine blue (Lillie, 1929, in Humason, 1967). Acid and alkaline phosphatase tests were done by Gomori's modification according to Pearse (1960).

To determine the natural food and feeding habits, gut contents were examined immediately after capture, or specimens were frozen for subsequent examination. Also the feeding habitat was observed by SCUBA diving. Food movement and digestion rates were observed in specimens from 150 to 200 mm SL which were fed whole, small mussels less than 20 mm (shell length), or the visceral mass of larger mussels. Cunners were either fed daily or were starved for 7 days prior to experimentation. Fish were allowed to feed voluntarily on a cluster of mussels during the ½- to 1-hr periods. Uneaten mussels and broken shells were removed after the feeding period. Carmine, Chinese ink, or ultramarine blue were injected into the visceral mass as indicators. Fishes were killed by severing the spinal cord at the base of the skull, at 1-hr intervals from 0 to 36 hr after feeding. Autopsy was done immediately after sacrificing the fish in order to locate the position of the food. All pH values of the gut lumen were determined from narrow range pH papers.

Ten adults (180-240 mm SL) and 6 juveniles (30-34 mm SL) were used for histological and histochemical studies, and 68 specimens (30-300 mm SL) for analyses of gut contents.

RESULT

Morphology and Histology of the Alimentary Tract

As reported by previous authors for other labrids (Barrington, 1942; Suyehiro, 1942; Al-Hussaini, 1947b; Gohar and Latif, 1959,

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1961), the alimentary tract of the cunner consists of neither a morphologically nor a physiologically differentiated stomach. The alimentary tract can be divided into several regions; the preesophageal cavities, esophagus and esophageal-intestinal valve, intestine, rectal valve and rectum, and associated organs.

Preesophageal Cavities

This region has three parts: the mouth, buccal cavity, and pharyngeal cavity (Figure 2).

MORPHOLOGY.—Cunners have large caninelike or incisorlike teeth on the premaxillary and dentary bones. The protrusible premaxillary bears three or four rows of conical teeth directed posteriorly, as are the two or three rows of dentary teeth. The most anterior rows of both premaxillary and dentary teeth are two to four times larger than the other rows. Also, the anterior most teeth are larger than the following ones on the same row. Teeth from 15 specimens (130-230 mm SL) numbered 32-66 on the premaxillary and 21-44 on the dentary. The number of teeth increases with the size of the fish. Developing teeth were found at the edges of the older teeth on all tooth bearing bones. Longitudinal ridges of mucous membrane extended from the vomer to the pharynx on the roof of the buccal cavity. The buccal valve is located posterior to the buccal cavity (Figure 2). There are no teeth on the vomer and palatine bones. A large tongue covers the entire floor of the anterior pharyngeal cavity and forms a sublingual cavity. The pharyngeal cavity is bounded laterally by gill arches. A yellowish brown mucous layer, patchlike and thicker than that in the buccal cavity, covers the entire roof and posterior part of the floor. Strong mucous secreting activities occur in this area. Both the upper and lower pharyngeal teeth are surrounded partially by this mucus. The pharyngeal teeth (upper 41-59, lower 28-56) are multitubercular and molariform. A pair of upper pharyngeal bones attach to the epibranchial bones and a triangular lower pharyngeal plate is attached to the basibranchial bones.

HISTOLOGY.—The mouth is lined with a stratified epithelium of the transitional type without a cuticular surface. The mucosa is thrown into ridges which start at the inner side of the protrusible lips (Figure 3) and extend to the esophagus. Taste buds lie on the crest of the ridges, and basophilic mucous secreting cells occur at the sides and bases, but the large acidophilic mucous cells present in the skin are absent here (Figure 3). Polyhedral cells and low-columnar cells constitute the rest of the layer. The mucosal layer and

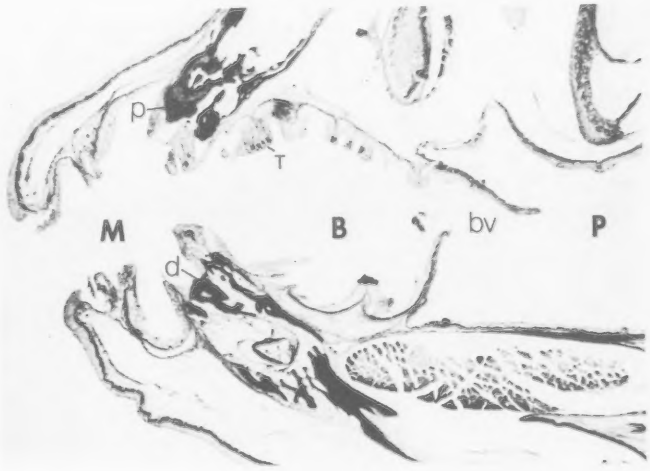

FIGURE 2.—Mouth (M), buccal cavity (B), and pharyngeal cavity (P) of a 40-mm SL juvenile cunner (× 40; power of observation). bv, buccal valve; d, dentary teeth; p, premaxillary teeth; T, taste bud.

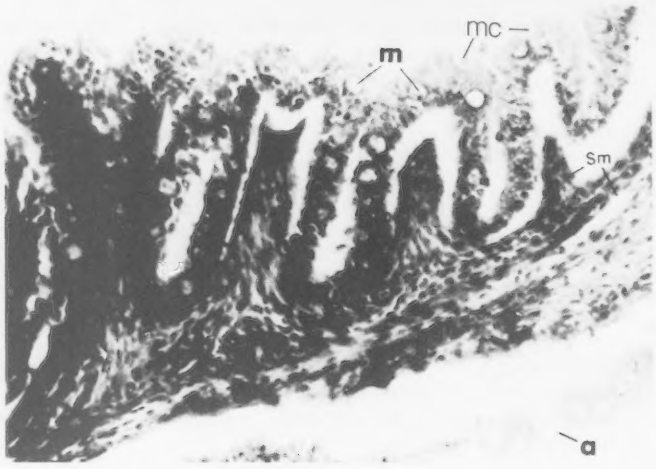

FIGURE 3.—Distribution of mucous secreting cells at sides and base of the mucosal ridges of protrusible lip in cunner (× 250, x.s.). a, acidophilic mucous secreting cell; m, basophilic mucous secreting cell; mc, mucosal layer; Sm, submucosa.

the ridges are deepest in the region of the teeth where the mucosa may be over 10 cells thick. Elsewhere, the mucosa is four to six cells thick, except for the sublingual area and the lateral side of the buccal cavity where a thickness of only one or two cells may prevail. The lateral mucosa of the pharyngeal cavity (the internal epithelium of the opercle) is one cell thick and is entirely constructed of mucous secreting cells attached to the opercle by a thin layer of connective tissue (Figure 4). The ridges or mucosal folds are more prominent on the midlines of the roof and floor of the pre-pharyngeal regions. There are no ridges on the surface of the sublingual cavity. The submucosa is a layer of fibrous connective tissue under the mucosa. It is continuous throughout this region, and the thickness is closely correlated with the depth of the mucosal folds.

Taste buds occur from the inside of the lips to the pharyngeal teeth (Figures 3 and 5) and occasionally are found on the gill arches. No taste buds were observed on the external side of lips, anterior sublingual cavity, or the lateral wall of the pharyngeal region. The aggregation of taste buds is closely related to the papillae

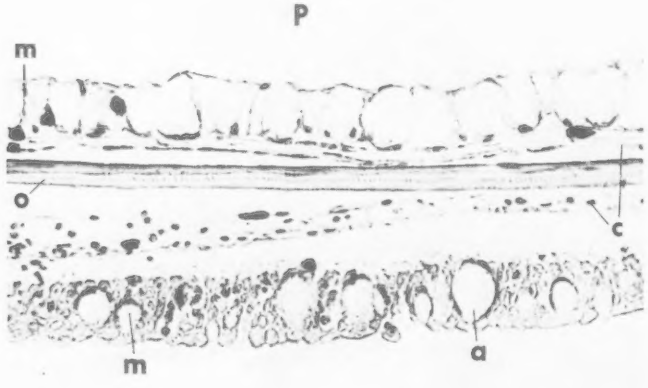

FIGURE 4.—Lateral mucosa of the pharygeal cavity (P) entirely covered with mucous secreting cells in cunner (× 250, x.s.). a, acidophilic mucous secreting cells; c, connective tissue; m, basophilic mucous secreting cell; o, opercle.

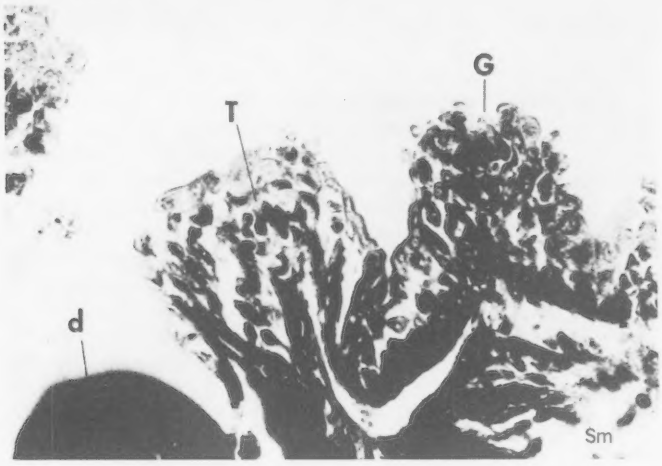

FIGURE 5.—Taste buds (T) on the mucosa of protrusible lip of cunner (× 400). d, dentary tooth; G, gustatory pore; Sm, submucosa.

folds, i.e., to the middle lines of this region and to the teeth. The taste bud is an ovoid structure of epithelial cells (Figure 5). A gustatory pore is present at the tip of each taste bud. A thickening of the submucosal layer contains the nerve fiber and forms the base of the taste bud.

Basophilic mucous secreting cells continue from the external lips and appear throughout this region. Mucous cells increase in numbers posteriorly. The lateral surface of the pharyngeal cavity and the ridges among the teeth are covered by mucous secreting cells. Beneath the basal membrane of the mucous layer, the submucosa is formed of a thick layer of collagen fibers toward the posterior part of the pharyngeal cavity. The areolar connective tissue of the tunica propria and submucosa are similar in this region. Lymphocytes and granulocytes are apparent in the submucosa of the ridges among the pharyngeal teeth. Circular muscles which connect to the head bones are external to the areolar connective tissue.

The epithelium and submucosa of the tongue are similar to that of the pharyngeal cavity but are much more compact (Figure 6). Posteriorly,

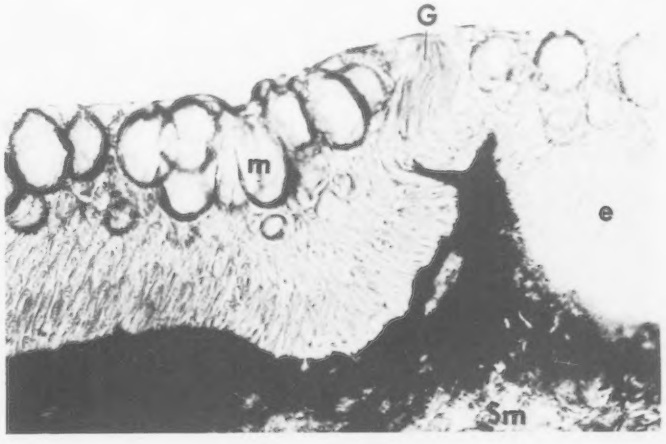

FIGURE 6.—Mucosa (e) and submucosa (Sm) of the tongue of cunner with hairlet sensory organ (× 400). e, epithelium (mucosa); G, gustatory pore of hairlet sensory organ; m, basophilic mucous secreting cells.

the submucosa below the dorsal epithelial layer is thicker than beneath the ventral layer. A flaplike structure directed posteriorly was observed on the ventral side of the tongue. Sensory organs, consisting of numerous sensory cells provided with hairletlike processes, occur on the tongue (Figure 6) and open into the pharynx through a gustatory pore.

Esophagus and Esophageal-Intestinal Valve

Posterior to the pharyngeal teeth, the pharynx constricts markedly to form a short muscular tube, the esophagus, which opens directly into the intestine through a muscular valve. Distinct longitudinal ridges (Figure 7) continue from the pharynx to the esophageal-intestinal valve and then diverge in the intestine. There are no transverse connecting cores between the longitudinal folds. These folds branch shortly anterior to the esophageal-intestinal valve (Figure 8). The mucous cells in the epithelium disappear in this region (transitional zone). This is more prominent in small specimens (less than 40 mm SL) than in larger specimens (200 and 210 mm SL).

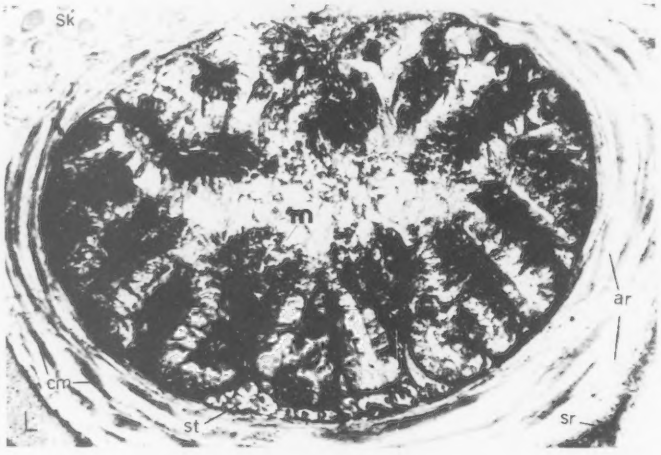

FIGURE 7.—Longitudinal ridges of the anterior esophagus of a 40-mm SL juvenile cunner (× 40, x.s.). ar, areolar connective tissue; cm, circular muscle layer; L, liver; m, mucous; Sk, skeletal muscle; sr, serosa; st, striated muscle.

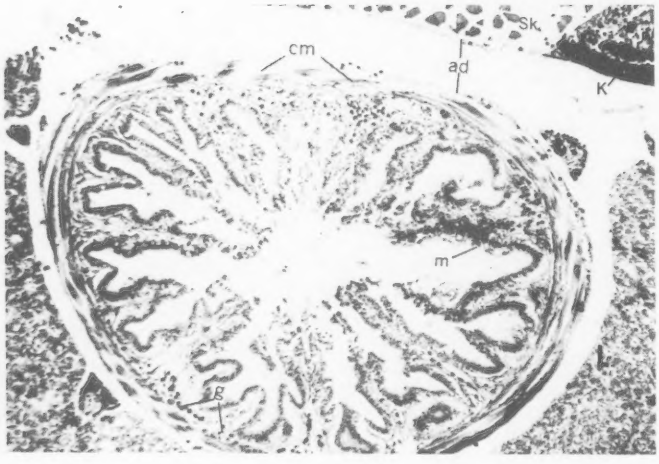

FIGURE 8.—Transitional zone anterior to the esophageal-intestinal valve in the esophagus of a 40-mm SL cunner (× 40, x.s.). ad, adventitia; cm, circular muscle layer; g, granulocyte; K, kidney; L, liver; m, mucous secreting cell; Sk, skeletal muscle.

MUCOSA.—The epithelium of the anterior esophagus is a modified transitional type (Figure 9) with large mucous cells extending to various depths from the surface. While the esophagus proceeds posteriorly, the stratified epithelium gradually becomes simple columnar in the transitional zone between the esophagus and intestine. The flattened nucleus of each mucous cell is pressed against the base by the large vacuole. The mucous secreting cells do not narrow appreciably where they open into the lumen. They can occupy nearly the entire surface and thickness of the epithelium, and they decrease in numbers from anterior to posterior. Also, smaller mucous cells with large vacuoles filled with mucous were found among the basal cells in the anterior half of the esophagus (Figure 9). The columnar epithelium appears gradually while the mucous cells decrease toward the transitional zone. The large oval nuclei of columnar cells are located at the basal level under the level of the mucous cells in the transitional zone. The basal cell layer appears to maintain a uniform thickness throughout the esophagus. These cells are small with relatively large nuclei. Occasionally, taste bud like structures were found at the tip of major folds in the most anterior part of the esophagus. No cilia are present on the epithelium of the esophagus. The mucosal layer of the esophageal-intestinal valve is similar to that of the transitional zone, except for an increased number of mucous secreting cells, especially, in the distal portion of the valve (Figure 10).

SUBMUCOSA.—The submucosal layer is an areolar connective tissue between the epithelium and the muscularis. The stratum compactum (Figure 9) is a layer of compacted fibrous connective tissue attached to the basal membrane of the epithelium. The rest of the areolar connective tissue is highly vascularized. Longitudinal bundles of striated muscles extend from the pharynx to the base of the esophageal-intestinal valve in the connective tissue. Also, in the anterior half of the esophagus, these longitudinal muscles are dispersed irregularly up to half of the depth of the folds in the submucosa (Figures 7, 9). Collagen fibers constitute the framework of the submucosal layer. The vascular system is scattered in this framework, and leucocytes, lymphocytes, fibrocytes, and granular cells are present. The granulocytes first appear in the posterior half of the esophagus (Figure 8). The submucosa becomes much thicker on both sides of the esophageal-intestinal valve. Increasing numbers of granulocytes appear in the submucosa of the intestinal side of the valve.

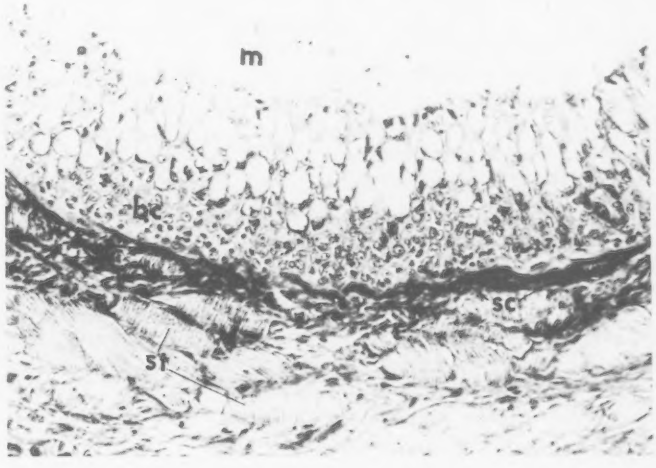

FIGURE 9.—Mucosa and submucosa of the anterior esophagus of a 200-mm SL cunner (× 400, x.s.). m, mucous secreting cell; sc, stratum compactum; st, striated muscle.

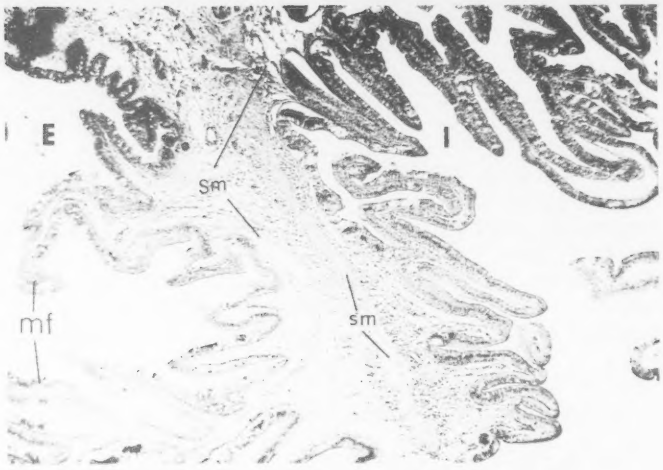

FIGURE 10.—The esophageal-intestinal valve of a 240-mm SL cunner (× 40). E, esophagus; I, intestine; mf, mucosal fold; sm, smooth muscle; Sm, submucosa.

MUSCULARIS AND SEROSA.—A very thick circular layer of striated muscles continues from the pharynx forming the external muscular layer of the esophagus (Figures 7, 8). It is invaded by elements of the vascular system accompanied by connective tissue; thus it is a loose rather than a compact layer. This muscularis appears to decrease in thickness posteriorly toward the esophageal-intestinal valve, where it forms a triangular, sphincterlike structure along the base of the valve fold. The basal muscularis of the valve is formed of smooth and striated muscles and retains significant connective tissue components. Leucocytes, fibroblasts, and a few granular cells also occur in this connective tissue. The distal portion of the valve contains a single undivided smooth muscle layer (Figure 10). This ring is continuous with the circular muscle layer of intestine.

The anterior esophagus is attached to the associated skeletal muscles by a layer of adventitious tissue. After passing through the transverse septum, the esophagus separates from the visceral wall ventrally. The dorsal wall of the midesophagus is attached to the kidney and skeletal muscles by a thin layer of adventitia (Figures 7, 8). The ventral side is covered by the peritoneal lining (serosa) and is separated from the circular muscularis by a varying thickness of areolar connective tissue (Figure 7). Posteriorly, the serosa increases in thickness in the vicinity of the esophageal-intestinal valve.

Intestine

The intestine starts posterior to the esophageal-intestinal valve and extends to the rectal valve. The intestine can be divided into four sections (Figure 1). The first section (I) begins dorsally and proceeds posteriorly and slightly to the left. It turns ventrally and extends anteriorly to the right as section II. The second loop curves abruptly posterior at about the level of the intestinal bulb. The third section (III) proceeds posteroventrally to an S-shaped loop which is connected by a short, straight portion of the intestine to the rectum. Intestinal veins from sections I, II, III, and the S-loop are associated with the anterior mesenteric vein and the posterior mesenteric vein from the rectum (Figure 1). The intestine has a consistent histological organization throughout its length with minor cytological variations. The mucosa is more complex in the intestine than in the esophagus and has zigzag folds as well as secondary and tertiary folds. The intestinal bulb is a dilation of the anterior portion of the intestine where the latter joins the esophagus. The mucosal folds of the intestinal bulb are deeper than in other portions of the intestine. There are four distinguishable layers

in the intestinal wall: mucosa, submucosa, muscularis, and serosa (Figure 11).

MUCOSA.—The epithelium of the mucosa consists mainly of columnar absorptive cells and goblet cells. The columnar absorptive cells of the cunner are similar to those of the stomachless cyprinids described by Al-Hussaini (1949a). The epithelium can be divided into the same four regions: the free border, the subborder, the supranuclear, and the infranuclear zones (Figures 12, 13, 14). The free border of the mucosa is sharply defined throughout the intestine. The striated border (or subborder) in the active digestive epithelium (Figure 14) is slightly thicker than in the inactive (Figure 13) epithelium. It stains intensively with periodic acid-Schiff (PAS) (Figure 15) and shows very prominent digestive effects in the active epithelium (Figure 14). In the resting cell of starved fish, the cytoplasm can be divided into a subcuticular zone and a layer of fine granules (Figures 12, 13). The subcuticular zone in starved fish is a compara-

FIGURE 11.—Mucosal folds of the posterior section I of the intestine of a 240-mm SL cunner (× 100, x.s.). cm, circular muscle layer; lm, longitudinal muscle layer; mc, mucosa; ms, muscularis; Sm, submucosa; sr, serosa.

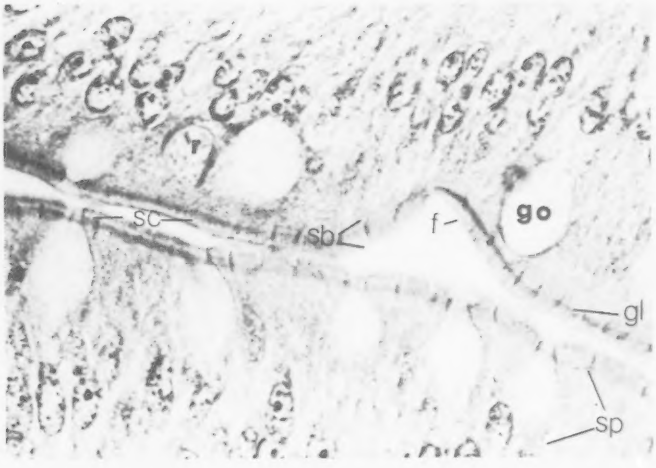

FIGURE 12.—Free border (f) of the columnar epithelium of the intestine (I) of cunner (× 1,000). gl, granular layer; go, goblet cell; r, rodlet cell; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

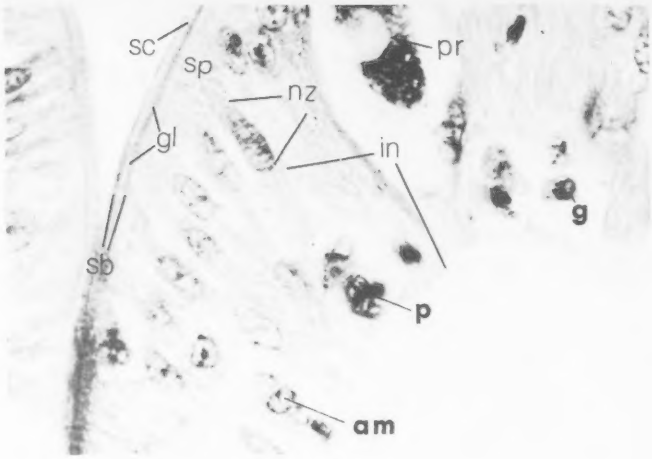

FIGURE 13.—The mucosal epithelium of the intestine (II) of cunner (× 1,000). am, ameobocyte; g, granulocyte; gl, granular layer; in, infranuclear zone; nz, nuclear zone; p, polymorpho-leucocyte; pr, parasite; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

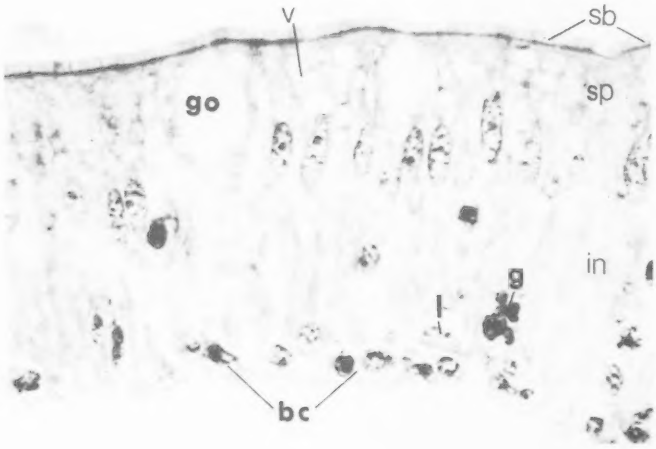

FIGURE 14.—The active absorption epithelium of the posterior intestine (III) of cunner (× 1,000). bc, basal cells; g, granulocyte; go, goblet cell; in, infranuclear zone; l, lymphocytelike cell; sb, striated border (subborder); sp, supranuclear zone; v, vacuole.

tively clear region and has a higher affinity for eosin Y than the other regions. Cell membranes are indistinguishable or indistinct resulting in a homogeneous appearance. The granular layer (Figures 12, 13) continues to the supranuclear zone and is more basophilic than other parts of the nonnuclear zones. In well-fed specimens, the resting cells have the same appearance as in the starved ones. Numerous unstained vacuoles are present in the subborder and the supranuclear zone of the active cells of the absorptive epithelium (Figure 14). In many cases, vacuoles also appeared in the infranuclear zone. The granular cytoplasm of the active cells forms a strong basophilic network around the vacuoles.

The nuclei of absorptive cells are ellipsoidal with abundant basophilic granulation and a large centrally located nucleolus. The nuclei are located at the middle or the basal third of the columnar epithelium at the intestinal bulb and then gradually move to the upper third of the epithelium posteriorly. As a result, the depth of the supranuclear zone decreases slightly posteriorly. The nuclei of the developing absorptive cells, the goblet cells, and other non-

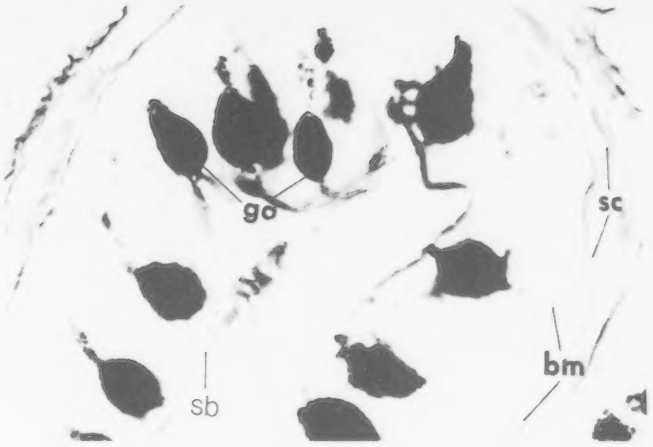

FIGURE 15.—PAS demonstration of goblet cells (go) in the intestinal epithelium (II) of cunner (× 1,000). bm, basement membrane; sb, subborder; sc, stratum compactum.

absorptive cells are found always in the infranuclear zone. The mucous secreting cells in the intestine (Figures 12, 14, 15) differ morphologically from the mucous cells in the preesophagus (Figures 3, 4, 6, 9). They are elongate with a thin neck extending to the surface and a rodlike root extending straight down to the infranuclear region (Figures 12, 15). The ovoid nucleus of the mucous cell sits at the bottom of this root. Only the mucous secreting cells near the esophageal-intestinal valve of the intestinal bulb are the same shape as the mucous secreting cells of the esophagus. Mucous cells also appear to develop in the infranuclear region and grow or extend gradually to the lumen.

A very distinct type of cell, the rodlet cell, a term introduced by Bullock (1963) for these cells in salmonids, was also found in the mucosa of the cunner (Figure 12). They are distributed throughout the intestine but are more abundant in sections II and III. They are most abundant in the bile duct (Figure 16) and inner epithelium of the gallbladder (Figure 17). The elongate, oval, rodlet cells are usually located in the supranuclear region of the mucosa and

FIGURE 16.—The bile duct (bd) of cunner with abundant rodlet cells (r) (× 400). g, granulocytes; Sm, submucosa.

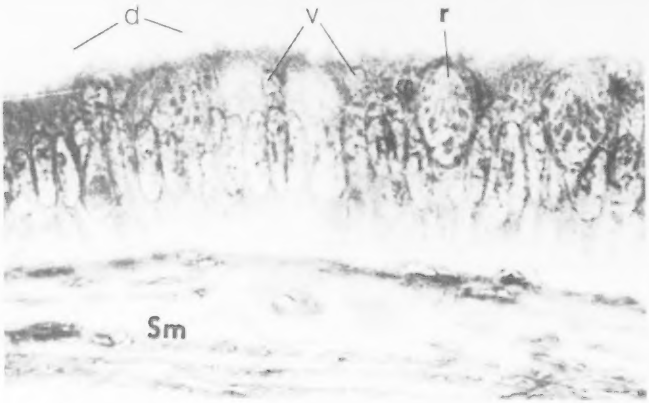

FIGURE 17.—Epithelium in the gallbladder of cunner showing rodlet cells (r), vacuoles (v), and digitiform processes (d) (× 1,000). n, nucleus of rodlet cell; Sm, submucosa.

are in direct contact with the lumen. The cytoplasm of the rodlet cells (Figure 17) consists of many granules with a threadlike structure extending from each granule to the distal end of the cell. These granules are acidophilic and stained deeply with PAS technique. A large nucleus is near the base of the cell. Various developmental stages of the rodlet cells can be observed in some of the bile duct preparations.

SUBMUCOSA.—The submucosa, which forms the core of the mucosal folds of the intestine, is a single homogeneous layer of fibrous connective tissue between the epithelium and muscularis (Figure 11). The stratum compactum, a thin layer of dense connective tissue, can be identified just beneath the mucosa (Figure 15). The collagenous fibers in the submucosa are more dense at the posterior portions of the intestine and rectum. Several cell types are scattered in the collagenous tissue. The most abundant cells are fibroblast of different stages. The young fibroblast has an ovid nucleus and basophilic astral cytoplasm (Figure 18). The fibrocytes (mature fibroblasts) are most easily seen in the submucosa of the top of the folds. It is very difficult to see any cytoplasm in these fusiform cells. The nuclei of fibrocyte is elongate or oval in shape with a

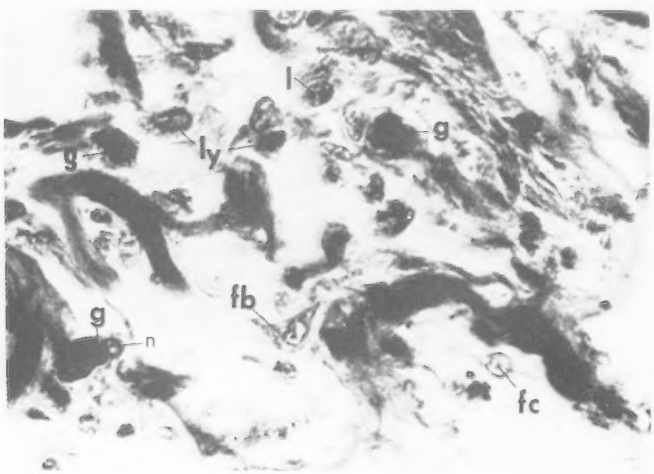

FIGURE 18.—The submucosa of the intestine of cunner (× 1,000). fb, fibroblast; fc, fibrocyte; g, granulocyte; l, lymphocytelike cell; ly, lymphocyte; n, nucleus of granulocyte.

very dense eccentric nucleolus (Figure 18). Granular wandering cells occur in the mucosa, submucosa, and muscularis (Figures 13, 14, 18), and are most abundant in the submucosa at the base of the mucosal folds. In the mucosa they are found in both the supranuclear and infranuclear zones. These cells are packed with basophilic granules. The nuclei are always pushed to the cell margin by the large granules (Figure 18). Some of the granulocytes present in the mucosa have very large compact inclusion bodies (Figures 14, 18). The polymorphonuclear leucocytes represent one type of wandering cell (Figure 13). Its nucleus has two or three lobes, and there are very fine neutrophilic granules in the cytoplasm. These leucocytes were encountered only in the infranuclear zone and the submucosal layer of the fold. A lymphocytelike type of cell was encountered also in the infranuclear zone or the base of the epithelium. This type of cell has two nucleoli in the clublike nucleus and very little cytoplasm (Figures 14, 18). They also were encountered in the submucosa occasionally. The typical lymphocytes with large nuclei and thin basophilic cytoplasm were found in the submucosa (Figure 18). At least one type of amoebocyte (Figure 13) was found in the mucosa and submucosa. This type of amoebocyte has a round nucleus with karyosomes applied to the nuclear membrane and rays extending from the nucleolus which is often eccentric. Numerous spherical granules and vacuoles occur in the cytoplasm. There are no significant differences in the distribution or types of wandering cells in the submucosa throughout the intestine.

MUSCULARIS AND SEROSA.—The typical vertebrate muscularis of inner circular and outer longitudinal smooth muscle prevails in the intestine of the cunner (Figure 11). A very thin layer of smooth, longitudinal muscle fibers (no more than two cells thick) can often be seen inside the circular muscle layer. These fibers appear at random in the first three sections of the intestine and become more prominent (two to four cells thick) from the S-loop to the rectal valve. A nerve plexus usually can be found between the muscle layers. The serosa is of a more uniform thickness than that in the esophagus and abuts directly on the extended muscularis.

Rectal Valve and Rectum

A muscular flap valve is present at the juncture of the intestine and rectum. The rectal valve is formed by a folding of the circular muscle layer and is not a sphincter valve of thickened muscularis. The two layers of the fold are separated by connective tissue (Figure 19). This layer of connective tissue contains granular cells which are more abundant in the submucosa of the rectal side of the valve. The

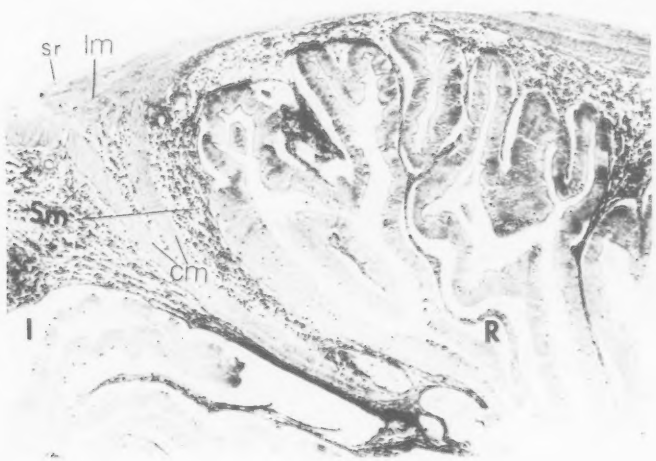

FIGURE 19.—Intestinal-rectal value of a 210-mm SL cunner (× 40, l.s.). cm, circular muscle; I, intestine; lm, longitudinal muscle; R, rectum; Sm, submucosa; sr, serosa.

nerve plexus, blood vessels, and longitudinal muscles merge in the connective tissue at the base of the rectal valve. Some bundles of the circular layer remain associated with the longitudinal layer at the base.

The rectum proceeds posteroventrally to the anus. In the anterior part of the rectum, the absorptive cells of the mucosa show more vacuoles in the supranuclear zone in well-fed specimens. The submucosal layer has more granulocytes than the intestine. The vascular system is also more prominent. The longitudinal muscle layer just inside the circular layer is distinct posterior to the rectal valve. Posteriorly in the rectum, the number of mucous cells decreases gradually and then increases around the anus. The epithelium of the rectum continues to the anal papillae (Figure 20). Granulocytes are the most abundant cell type in both the internal folds and external papillae of the anus. The circular muscle layer at the end of the rectum forms a sphincterlike structure. The longitudinal muscles and the nerve plexus radiate into the connective tissue around the anus. The serosa is replaced by an adventitia composed of an extensive development of fibrous connective tissue.

Associated Organs

GALLBLADDER—The gallbladder is half embedded into the liver and opens anteriorly into the intestinal bulb via the common bile duct. The bile is usually dark green and has pH values between 7.5 and 8.5. The fullness of the gallbladder was usually inversely correlated to the fullness of the intestine. It is a highly elastic structure which becomes more elongate when full. The columnar epithelial cells of the mucosa have fingerlike projections extending toward the lumen (Figure 17); however, there are no mucosal folds. A small vacuolelike structure present in each columnar epithelial cell of the gallbladder at the supranuclear zone is stained intensively in fast green, analine blue, and PAS preparations. Rodlet cells are present and are more concentrated in the bile duct than in the bladder itself (Figures 16, 17). The submucosa is a rather thin layer of very dense collagenous tissue in which a few granulocytes, fibrocytes, lymphocytes, and capillaries are present. Smooth muscle cells occur beneath the serosa, but their arrangement (spiral, random, etc.) could not be ascertained. The mucosa and submucosa of the bile duct are similar to those of the intestine; but mucous secreting cells are completely absent. The rodlet cells in the bile duct increase abruptly in number near its entrance into the intestine.

PANCREAS.—The pancreas is diffuse, forming small nodules, and consists of numerous small lobules scattered with fat and vascular

FIGURE 20.—External surface of the anal papillae of a 210-mm SL cunner (× 400). a, acidophilic mucous secreting cell; g, granulocyte; m, basophilic mucous secreting cell; Sm, submucosa.

tissue in the mesentery (omentum). It is also dispersed into the liver in the vicinity of the bile duct. Granulocytes are very abundant around the pancreas and the hepatopancreatic complex. The pancreatic duct joins the bile duct near the entrance of the latter into the intestine. The mesenteric membranes are more prominent during late summer when fatty tissue accumulates after the active feeding season.

LIVER.—The liver is divided into three lobes. The central lobe, the largest one, is triangular in shape and the tip continues to the loop of sections I and II of the intestine (Figure 1). In large specimens this lobe elongates posteriorly and covers the spleen ventrally. Two smaller lobes extend lateral-dorsally to cover most parts of the esophagus and the intestine bulb.

Histochemistry

The PAS technique intensely stains the free border and subborder of the intestinal epithelium as well as the basal membrane and goblet cells (Figure 15). The goblet cells and the granules in the granulocytes and amoebocytes give the strongest PAS reaction. Alcian blue and toluidine blue methods stained only the mucoid contents of the goblet cells, indicating the presence of acid mucopolysaccharide and mucin. None of the methods showed any secretory activity by the rodlet cells. There were no distinct differences in these reactions in the different portions of the intestine.

Throughout the alimentary tract the pH value ranged between 7.0 and 8.5. Acidic conditions were not found in either fed or starved specimens. Also, acid phosphatase tests were negative in all cases. Alkaline phosphatase can be demonstrated at the border of the epithelium throughout the gut except anterior to the esophageal-intestinal valve (Figure 21). No positive reaction for alkaline phosphatase was found in the epithelium of the gallbladder, bile duct, or pancreatic duct. Alkaline phosphatase activity was intense in the intestinal bulb and rectal valve, and it was most obvious on the distal surface of the intestinal folds in the presence of food particles.

Food and Feeding Habits

Cunners at East Point are abundant inshore during the summer and may feed intertidally during high tide. Cunner were observed swimming in the kelp beds and using the kelps *Agarum*, *Alaria*, *Laminaria*, etc. as shelter. Juveniles (less than 100 mm SL) moved intertidally or into tide pools where they use brown algae *Ascophyllum* and *Fucus* as shelter. The intestinal contents of 68 specimens (Table 1) show that the cunner is primarily carnivorous

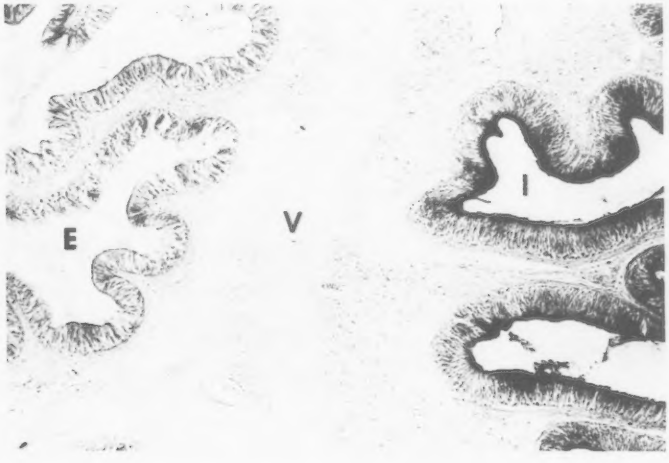

FIGURE 21.—Alkaline phosphatase test of the esophageal-intestinal valve (V) of a well-fed 180-mm SL cunner (× 100, l.s.). E, esophagus; I, intestine.

TABLE 1.—Gut content of 68 cunners, *Tautogolabrus adspersus*, from Nahant, Mass.

Standard length (mm)	30-50		100-225		230-300	
Age group (years old)	0+ -1+		1+ -4+		4+ -6+	
Specimens with food	8		27		10	
Occurrences	No.	%	No.	%	No.	%
Mussels (*Mytilus*, *Modiolus*)			27	100.0	5	50
Bivalve larvae			5	18.5		
Gastropod (*Littorina*, *Thias*, etc.)			9	33.3	1	10
Barnacles (*Balanus*)			11	40.7	5	50
Sea urchin (*Strongylocentrotus*)			7	25.9	3	30
Crustaceans (amphipod, copepod, isopod, etc.)	8	100.0	3	11.1	1	10
Decapod (crabs)			1	3.7	3	30
Tunicate (*Amaroucium*)			2	7.4	2	20
Polychaete			1	3.7		
Seaweeds with epiphytic animals (Bryozoa, Hydrozoa, etc.)	1	12.5	9	33.1	3	30
Intestinal parasites						
Acanthocephala			3	11.1	3	30
Nematode					1	10

during the active feeding season (May to September). The foods were mainly mussels *Mytilus edulis* and *Modiolus modiolus*, barnacle *Balanus balanoides*, tunicate *Amaroucium* sp., and small specimens of the green sea urchin, *Strongylocentrotus drobachiensis*. Entire gut contents may consist entirely of one species mentioned above or, usually, of a mixture of these foods. Also some seaweeds, such as *Chondrus*, *Laminaria*, *Polysiphonia*, and *Porphyra*, were often associated with the animal foods. Occasionally, crabs, amphipods, and microcrustaceans (copepods, etc.) were found. In juvenile specimens (less than 40 mm SL), amphipods and microcrustaceans were the main food. The food was well triturated in most cases although entire mussels (less than 20 mm shell length) and, in one specimen, a crab leg longer than the first portion (I) of the intestine (Figure 1) was observed. In aquaria, cunners found their food by sight. They may pick up a whole mussel from the bottom or catch falling ones as they are introduced into the tank. Also, they removed small mussels one by one or as batches from clusters. Occasionally, the food, as well as mussel shell fragments, was spat out and reswallowed. Feeding activities greatly decreased during the winter when water temperature in the aquaria dropped below 4°-6°C. This was especially noticeable in the large individuals caught during the previous summer.

Movement and Digestion of Food Materials within the Gut

The gut in unfed cunner had little or no fluid in the lumen. The intestine and rectum were rather constricted with thick walls. During feeding, small mussels were picked up with the jaw teeth and triturated by the pharyngeal teeth before entering the esophagus. The crushed mussels were pushed back into the eophagus and intestine due to continuous food ingestion during the feeding period. Feeding continued until the food was packed up to the sigmoid loop (Figure 1) and occasionally even to the rectal valve or rectum. The intestinal lumen distends and the wall in turn becomes thinner when the gut is full. The shells of one feeding period always moved as a unit separate from the next feeding period. A period of 10-14 hr was required for mussel shells from a single feeding period (½-1 hr) to pass through the alimentary tract. The compact mass of shells moving along the intestine sometimes straightened the S-loop. Food storage in this stomachless fish was achieved mainly by the intestine anterior to the S-loop. The loop between sections I and II formed a saclike reservoir (Figure 1). Ingested foods remained in section III longer than in the other loops suggesting that this section may be responsible for more digestion and absorption than the other sections. Fluid developed in the lumen during and for a short while after the presence of shells. The amount of bile secretion depended on the quantity of food ingested. The volumes could not be estimated in the present study. In most fish with a full gut which were dissected immediately after capture, the gallbladders were shrunken or contained brownish fluid. The entire range of pH value found in all parts of the gut, both empty and full, was 7.0-8.5, thus suggesting alkaline digestion in the cunner gut.

DISCUSSION

Digestive System

The morphology of the mouth and buccal and pharyngeal cavities of the cunner is similar

to the labrids described by Al-Hussaini (1947b). The buccal valve (Figure 2) is similar to that of *Julis aygula* reported by Gohar and Latif (1961), except for the obvious thickening of the mucous layer of the anterior surface in juvenile cunners. The rather short relative length of the gut of the cunner, i.e., the postpharyngeal portion of the alimentary tract, is about 0.8-1.0 of standard length. The extensive vascularization of the serosa and adventitia of the rectum and the strong alkaline phosphatase activity of the rectal mucosa indicate that this region is very active in absorption and/or secretion. The S-loop of the intestine may be unique because it was not described for other labrids by Suyehiro (1942) and Gohar and Latif (1959, 1961) nor in some other stomachless fishes reported by Babkin and Bowie (1928) and Al-Hussaini (1949a). Bullock (1967) recorded a similar flexure in the posterior portion of the intestine of *Gambusia affinis*. The S-loop was somewhat straightened by large amounts of food in the lumen. Alkaline phosphatase tests show weak positive reaction in the S-loop. The significance of the loop may be mechanical rather than physiological. There are no successive constrictions of the intestine in cunner as observed by Gohar and Latif (1961) in *Pseudoscarus harid* and credited by those authors to *Julis aygula*.

Epidermal mucous secreting cells in the epithelium of the alimentary tract of cunner are mostly concentrated in the postpharyngeal cavity and the esophagus and on the anal papillae. These cells have no stalklike elongation at the bottom of the globule nor a narrow necklike structure before the open end (Figures 3, 4, 6, 9, 20) as do those of the intestine and rectum (Figures 12, 14, 15). No precise histochemical differentiation of these mucous cells was obtained. These different types of mucous cells have been reported by Al-Hussaini (1947a), Gohar and Latif (1961), Mohsin (1962), Bullock (1967), Western (1969), and Bucke (1971) in various fishes. Al-Hussaini (1949b) and Bullock (1963), following the terminology of Baker (1942), described the free border of the absorptive columnar cells in the intestine as divided into a superficial layer, a canal layer (or microvilli region), and a granular layer. These were also distinct in the cunner gut.

The rodlet cells are similar to those discussed by Bullock (1963) in the intestine of salmonid fishes and the pear-shaped cell of Al-Hussaini (1949b) recorded in *Gobio gobio*. These cells appeared throughout the gut except in the anterior intestinal bulb and the posterior rectum as in *Gambusia affinis* (Bullock, 1967). They are also found in the bile duct, gallbladder, and collecting duct of the kidney of the cunner. Bullock (1963) also described the appearance of rodlet cells in the kidney of *Catostomus* species. Al-Hussaini (1964) described the mitosis of the pear-shaped cell in *Cyprinus carpio*. He stated that experimental evidence indicated the pear-shaped cell may originate from goblet cells in *C. carpio* and *Gobio gobio* and from wandering blood or connective tissue cells in *Rutilus rutilus*. No comparable evidence of the division nor origin of the rodlet cells was found in this study. Bishop and Odense (1966) proposed that the pear-shaped cell may be a possible enzyme source in the intestine of the cod, *Gadus morhua*. But the negative phosphatase reactions of the rodlet cells in the cunner agree with Bullock's 1963 findings for salmonids. Different cytological or developmental stages of rodlet cells were observed in the mucosa of the bile duct, gallbladder, and intestine. The rodlet cells and their empty capsules, which have no distinct nuclei, were partially or entirely free from the mucosa of the bile duct. Occasionally, ejection of granules from the rodlet cells was seen. Rodlet cells have not been described in labrids prior to the present account. The question remains as to whether they are normal cells or coccidian parasites (Plehn, 1906).

The submucosal layer of the cunner gut is composed of a rather homogeneous fibrous connective tissue. There is neither muscularis mucosa nor lamina propria. The stratum compactum in various fishes has been discussed by Al-Hussaini (1947a), Burnstock (1959), Gohar and Latif (1961), Mohsin (1962), Bullock (1963), and Bucke (1971). In cunner it is a thin layer of regularly arranged fibers immediately beneath the mucosa. In oblique sections, fibrils can be seen passing from the

stratum compactum into the basement membrane.

Granulocytes in the submocosa of cunner can migrate to both the mucosa and the muscularis. According to Bolton (1933), basophilic granule cells occur in vast number in connective tissue throughout the gut of salmonid fishes. He suggested that they were histogenous cells developed from mesenchymal cells. Al-Hussaini (1949b) mentioned that two types of granulocytes also occurred in the intestine of a variety of fishes; some stained blue with Giemsa stain (*Trigla hirundo* and *Salmo trutta*), and others stained red with Giemsa (*Scarus sordidus, Rutilus rutilus, Gobio gobio, Atherina forskali, Cyprinus carpio, Crenilabrus melops,* and *Mulloides auriflamma*). Bullock (1963, 1967) stated that the granulocytes had varying results in staining reaction according to the different pH value of the stain, which was also true in this study. Large granulocytes, densely packed with granules which appear purplish with Giemsa stain, were abundant in the mucosa of cunner (Figure 14); smaller granulocytes were present which have smaller red staining granules in Giemsa (Figure 18). In addition, a type of granulocyte was observed in which the granules were condensed against the nucleus (Figure 13). Bullock (1963) found cells intermediate between granulocytes and globule leucocytes in salmonids but not in *Gambusia affinis* (Bullock, 1967). This intermediate type cell was found in various levels of the epithelium and submucosa of cunner intestine. No precise cytochemical demonstration of the possible relationships between granulocytes and leucocytes was obtained in this study. The wandering nature of the granulocytes did not seem to correspond in any way with the food contents in the intestine of the cunner. Aggregations of granulocytes occurred in the submucosa of the bile duct, rectal valve, and anal papillae of the cunner (Figures 16, 19, 20). Granulocytes similar to those in the intestine were also very abundant in the pancreas and kidney. The function of granulocytes may differ from species to species (Al-Hussaini, 1949b). The fine granules of the granulocytes were stained with PAS in many specimens of cunner. No evidence that granulocytes help in the absorption and transportation of digested foods was found in cunner as reported for other teleosts (Al-Hussaini, 1949b; Mohsin, 1962). Special aggregations of other types of wandering cells such as: polymorphonuclear leucocytes, lymphocytes, and amoebocytes were not found. The presence of amoebocytes (Figure 13) with large vacuoles and a large nucleus as observed in this study does not appear to have been previously recorded.

The muscularis of the esophageal-intestinal valve (Figure 10) and rectal valve (Figure 19) are formed of circular muscles. Gohar and Latif (1959, 1961) mentioned only one layer of muscle fibers in both the esophageal-intestinal valve and the rectal valve of the labrid *Julis aygula*. This is true in the esophageal-intestinal valve of the cunner, but in the rectal valve of the cunner, the circular muscle layer is folded and the two folds are separated by fibrous connective tissue. Al-Hussaini (1947a, 1947b) indicated two separate muscle layers in the ileo-rectal valve of the stomachless *Atherina forskali*, and Western (1969) described the same arrangement in *Cottus gobio*. It would appear that a more careful analysis of the intestinal-rectal (ileo-rectal) valve is required.

The differentiation of duodenum and ileum reported to occur in stomachless labrids (Gohar and Latif, 1961) was not found in the intestine of the cunner. Histological differentiation of the intestine was not mentioned by Curry (1939), Al-Hussaini (1947b), Khanna (1961), nor Bullock (1967) in other stomachless fishes. Thickening of the circular muscle layer at the anterior end of the rectum in cunner was similar to that in other species of stomachless fishes (Dawes, 1929; Al-Hussaini, 1947a, 1947b; Khanna, 1961; Gohar and Latif, 1961; Mohsin, 1962; Bullock, 1967). However, the additional thin layer of longitudinal muscle fibers present inside the muscularis in the rectum of the cunner was not reported by these investigators.

Al-Hussaini (1949b) reported that alkaline phosphatase was most abundant in the free border of the absorptive cell of three species of stomachless minnows—*Cyprinus carpio, Gobio gobio,* and *Rutilus rutilus*. Similar results were found along the free border of the

intestinal epithelium of the cunner in cells which are in direct contact with the food. An extremely strong alkaline phosphatase reaction was found in the intestinal bulb and anterior half of the rectum in the cunner. This reaction seems to be restricted to the free border of the epithelial layer of the intestine and rectum. Evidence of active rectal digestion also has been reported by Babkin and Bowie (1928), Ishida (1936), Al-Hussaini (1949b), Bullock (1967), and Western (1971) in other stomachless fishes.

The close association of the pancreas and bile duct in cunner observed in this study agrees with the observations of Gohar and Latif (1959) for another labrid, *Julis aygula*. Vacuoles (which stained intensively with fast green or with aniline blue) were observed in the supranuclear zone of the columnar epithelium of the gallbladder (Figure 17). No reference to this situation was found in the literature, and no data were acquired in this study to determine the function of these vacuoles.

Feeding Habits

Cunners are most active in daytime both in aquaria and in the field. Their activity decreased sharply during the night, the fish lying against objects on the bottom or hiding in crevices. Torpid behavior was observed during the day when the water temperature in the aquarium fell below 4°C. Bigelow and Shroeder (1953) and Green and Farwell (1971) also noticed that cunners become torpid during winter.

Cunner reach their greatest inshore abundance in summer (July- August). They were absent from the summer habitat from early November to late April. Observations made by SCUBA diving indicate that the offshore movements began as the water temperature dropped below 11°C (September 1971). A slight migration of cunner during the winter was postulated by Johansen (1925) and also reported by Bigelow and Schroeder (1953) and Green and Farwell (1971). Local fishermen reported the species to be present in deeper (more isothermal) waters in the winter. Juveniles tended to move into shallow water in early spring as reported by Johansen (1925). Some juveniles were collected during this season in brackish water at the Jackson Laboratory of the University of New Hampshire on Great Bay, N.H. This is in accordance with the statements of Johansen (1925) but is contrary to those of Bigelow and Schroeder (1953).

Cunners fed on both sessile (*Mytilus edulis* and *Modiolus modiolus*) and moving animals (*Fundulus heteroclitus*, *Gammarus oceanicus*, *Nephtys bucera*, *Nereis virens*, and *Cerebratulus lacteus*) in the laboratory and also acted as scavengers. Gut content analyses (Table 1) indicate that cunner are carnivorous rather than omnivorous in contrast to statements by Johansen (1925) and Bigelow and Schroeder (1953). There was no evidence that cunner actively consume algae in the aquarium even when starved. Algae found in the gut of cunner are always small and undigested and are frequently associated with digested epiphytic animals (bryozoans, hydrozoans, and larval molluscs). A change of prey was noted between juvenile and adult cunner (Table 1). Juveniles feed mainly on motile crustaceans in the water column, adults on sessile or sedentary animals. A few large, offshore specimens showed a further change in feeding habits.

In this study almost every adult specimen had mussel shells in the gut. Mussels *Mytilus edulis* and *Modiolus modiolus* cover the rock faces in the feeding habitat from which the cunner were taken. Most of the mussels eaten by cunner were less than 2 years old. Many other labrids are also mollusk feeders (Suyehiro, 1942; Al-Hussaini 1947b; Gohar and Latif, 1959). Randall (1967) recorded the food habits of 11 species of western Atlantic wrasses —all of which, except for the plankton feeding *Clepticus parrai*—tended to feed on hard-shelled invertebrates such as mollusks, crustaceans, and echinoderms. No algae were mentioned by these authors except that 5 out of 50 specimens of *Halichoeres poecilopterus* had seaweeds (*Ulva*, etc.) present (Suyehiro, 1942).

Feeding habits of cunner are related to their jaws, teeth, pharyngeal mill, and also the length of the intestine as reported for other stomachless fishes (Suyehiro, 1942; Al-Hussaini,

1949a; Gohar and Latif, 1961; Mohsin, 1962; Weatherley, 1963). The protrusible jaws of the cunner have sharp caninelike teeth which are adapted to catching, picking, and scraping animal foods. The strong muscles (hypobranchial and branchiomeric muscles) associated with the mouth can keep the jaws closed tightly, and quick movements of the body could help in detaching sessile organisms from the rocks. The molariform pharyngeal teeth of the cunner serve as a mill to grind up the hard shells of the ingested foods. The probability that well-developed pharyngeal teeth have taken over the mechanical function of the stomach among the stomachless fishes had been suggested previously by Barrington (1942, 1957), Suyehiro (1942), Al-Hussaini (1947b), and Gohar and Latif (1961).

Ingested foods passed rapidly through the buccal cavity and pharynx in the cunner as in most bony fishes. In the present study, the movement of mussels through the intestine of cunners fed in the laboratory, required 10 to 14 hr. Intact and alive mussels were found in all parts of the gut of freshly killed specimens both in the field and aquarium. Some of these mussels (less than 16 mm shell length) still were able to resettle. Field observations indicated that the largest individual mussels (over 100 mm shell length) were scattered on the surface of bare rocks 5 to 10 m below the tidal zone. However, the major population of the mussels formed patches or clusters in the intertidal zone. Perhaps cunner play a role in the vertical distribution of mussels.

No specific area of food storage was found in the cunner; the gut of fish which had been fed all they desired was completely packed with food, and it appeared that the entire intestine can serve as a storage organ while digestion is being completed. The intestinal bulb of stomachless fishes may substitute as a storage organ (Babkin and Bowie, 1928; Barrington, 1942; Al-Hussaini, 1947a; Khanna, 1961; Mohsin, 1962; Bullock, 1967).

Alkaline conditions (pH 7.0-8.5) prevailed throughout the gut in all specimens of cunners examined. In starved controls, there was little variation in pH value observed among regions of the intestine. However, in feeding fishes, the pH varied in a random fashion from region to region and showed no significant gradient. Phosphatase tests show a positive reaction for alkaline phosphatase, but negative for acid phosphatase. Intercellular digestion per se in the cunner is exclusively alkaline. Among other stomachless fishes, alkaline digestion was observed throughout the gut by Babkin and Bowie (1928), Ishida (1936), Barrington (1942, 1957), Al-Hussaini (1947a), Gohar and Latif (1959, 1961), and Bullock (1967).

Szarski (1956) discussed the advantages of alkaline digestion in stomachless freshwater fishes. He referred to the high biological value in retention of essential ions, which could also apply to the present species. Cunners feed mainly on shelled animals and the incidence of tooth damage is high. As is evident from having developing teeth along the edge of the old ones on the premaxillary, dentary, and pharyngeal bones. The apparent continuous regeneration and growth of teeth needs large amounts of calcium. The calcium supply cannot be obtained from the calcium carbonate of the animal shells due to the alkaline condition in the gut. Presumably, the calcium source is from the calcium pool of the viscera of the ingested animals.

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LITERATURE CITED

AL-HUSSAINI, A. H.
1947a. The anatomy and histology of the alimentary tract of the plankton-feeder, Atherina forskali Rüpp. J. Morphol. 80:251-286.
1947b. The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighbourhood of the Marine Biological Station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Al-Ghardaqa, (Red Sea) 5:1-61.
1949a. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: anatomy and histology. Q. J. Microsc. Sci. 90:109-139.
1949b. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: cytology and physiology. Q. J. Microsc. Sci. 90:323-354.
1964. On the nature of certain pear-shaped cells in the intestinal epithelium of fish. Bull. Inst. Egypte 40:23-32.

BABKIN, B. P., AND D. J. BOWIE.
1928. The digestive system and its function in *Fundulus heteroclitus*. Biol. Bull. (Woods Hole) 54:254-277.

BAKER, J. R.
1942. The free border of the intestinal epithelial cell of vertebrates. Q. J. Microsc. Sci. 84:73-103.

BARRINGTON, E. J. W.
1942. Gastric digestion in the lower vertebrates. Biol. Rev. (Camb.) 17:1-27.
1957. The alimentary canal and digestion. *In* M. E. Brown (editor), The physiology of fishes, Vol. 1, p. 109-161. Acad. Press, N.Y.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BISHOP, C., AND P. H. ODENSE.
1966. Morphology of the digestive tract of the cod, *Gadus morhua*. J. Fish. Res. Board Can. 23: 1607-1615.

BOLTON, L. L.
1933. Basophile (mast) cells in the alimentary canal of salmonoid fishes. J. Morphol. 54:549-591.

BUCKE, D.
1971. The anatomy and histology of the alimentary tract of the carnivorous fish the pike *Esox lucius* L. J. Fish Biol. 3:421-431.

BULLOCK, W. L.
1963. Intestinal histology of some salmonid fishes with particular reference to the histopathology of acanthocephalan infections. J. Morphol. 112: 23-44.
1967. The intestinal histology of the mosquito fish, Gambusia affinis (Baird and Girard). Acta Zool. (Stockh.) 48:1-17.

BURNSTOCK, G.
1959. The morphology of the gut of the brown trout (*Salmo trutta*). Q. J. Microsc. Sci. 100:183-198.

CURRY, E.
1939. The histology of the digestive tube of the carp (Cyprinus carpio communis). J. Morphol. 65:53-78.

DAWES, B.
1929. The histology of the alimentary tract of the plaice (Pleuronectes platessa). Q. J. Microsc. Sci. 73:243-274.

GOHAR, H. A. F., AND A. F. A. LATIF.
1959. Morphological studies on the gut of some scarid and labrid fishes. Publ. Mar. Biol. Stn. Al-Ghardaqa, (Red Sea) 10:146-186.
1961. The histology of the alimentary tract in representative scarid and labrid fishes from the Red Sea. Publ. Mar. Biol. Stn. Al-Ghardaqa, (Red Sea) 11:95-126.

GREEN, J. M., AND M. FARWELL.
1971. Winter habits of the cunner, *Tautogolabrus adspersus* (Walbaum 1792), in Newfoundland. Can. J. Zool. 49:1497-1499.

HUMASON, G. L.
1967. Animal tissue techniques. 2d ed. W. H. Freeman, San Franc., 569 p.

ISHIDA, J.
1936. Distribution of the digestive enzymes in the digestive system of stomachless fishes. Annot. Zool. Jap. 15:263-284.

JOHANSEN, F.
1925. Natural history of the cunner (*Tautogolabrus adspersus* Walbaum). Contrib. Can. Biol., New Ser., 2:423-467.

KHANNA, S. S.
1961 (1962). Alimentary canal in some teleostean fishes. J. Zool. Soc. India 13:206-219.

MOHSIN, M. D.
1962. Comparative morphology and histology of the alimentary canal in certain group of Indian teleosts. Acta Zool. (Stockh.) 43:79-133.

PEARSE, A. G. E.
1960. Histochemistry, theoretical and applied. Little Brown, Boston, 998 p.

PLEHN, M.
1906. Ueber eigentümliche Drusenzellen im Gefäß system und in anderen Organen bei Fischen. Annat. Anz. 28:192-203.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

STEEDMAN, H. F.
1960. Section cutting in microscopy. Thomas, Springfield, Ill., 172 p.

SUYEHIRO, Y.
1942. A study of the digestive system and feeding habits of fish. Jap. J. Zool. 10:1-303.

SZARSKI, H.
1965. Cause of the absence of a stomach in *Cyprinidae*. Bull. Acad. Pol. Sci. Ser. Sci. Biol. 4:155-156.

WEATHERLEY, A. H.
1963. Notions of niche and competition among animals, with special reference to freshwater fish. Nature (Lond.) 197:14-17.

WESTERN, J. R. H.
1969. Studies on the diet, feeding mechanism and alimentary tract in two closely related teleosts, the freshwater *Cottus gobio* L. and the marine *Palenophrys bubalis* Euphrasen. Acta Zool. (Stockh.) 50:185-205.

1971. Feeding and digestion in two cottid fishes, the freshwater *Cottus gobio* L. and the marine *Enophrys bubalis* (Euphrasen). J. Fish Biol. 3:225-246.

THE PYGMY WHITEFISH, *PROSOPIUM COULTERI*, IN WESTERN MONTANA

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ABSTRACT

The pygmy whitefish, *Prosopium coulteri*, is a glacial relict which has been considered to be the most primitive of coregonines. It is relatively abundant in lakes of western Montana and is undoubtedly an important source of food for Dolly Varden and lake trout. Compared to other members of its subfamily, it is characterized by low meristic counts. These counts differ somewhat in populations from Montana, Alaska, and Lake Superior.

Major food items consumed by the pygmy whitefish shift with availability but the main reliance is on cladocera and chironomid larvae and pupae. The annual growth in Flathead Lake, Mont., is greater than that in Lake Superior but below that in some Alaskan lakes. No males were found older than age III and no females beyond age IV. Many of the males mature at age I, a year earlier than most females. The spawning season is in December and January when the fish move into tributary streams. The species spawns in successive years. The fecundity of the Montana fish is similar to that of pygmy whitefish from other areas.

The pygmy whitefish successfully competes with other coregonines in reproduction by spawning at a later date and earlier age, and by having smaller eggs which yield more eggs per unit weight of fish. The small size and early age at maturity are considered adaptations developed for survival in cold and nutrient-poor water during glaciation.

The pygmy whitefish, *Prosopium coulteri*, is considered a glacial relict that survived in deep lakes after the retreat of the Wisconsin glaciation. Until the past 20 years the species was infrequently captured, or recognized when it was. It usually inhabits depths of over 30 ft and, because of its small size, escapes capture by most fishing gear. The present distribution is given as the Columbia, Fraser, Skeena, Yukon, and MacKenzie River systems, and both the Pacific Ocean and Bering Sea drainages of southwest Alaska (Heard and Hartman, 1966). In 1955 the report of this little fish from Lake Superior disclosed a remarkable case of disjunct distribution (Eschmeyer and Bailey, 1955).

Only in recent years has it been recognized how ubiquitous the pygmy whitefish is in western Montana. It was first reported in Montana by Schultz in 1941 from tributaries of Lake McDonald in Glacier National Park. The next report was from Bull Lake, a tributary to the Kootenai River (Weisel and Dillon, 1954). In the past 10 years it has been taken with small-mesh gill nets from Flathead, Ashley, Swan, Seeley, and the Little Bitteroot Lakes—all tributary to the Clark Fork River (Brown, 1971). Careful collecting will undoubtedly show the species to be present in many other glacially formed lakes in western Montana.

Our studies show the pygmy whitefish to be one of the most abundant fishes in Flathead Lake. According to Hanzel's 1968-71 extensive nettings, this species constituted 4.8% of the total catch; it ranked in order only below lake whitefish (*Coregonus clupeaformis*), peamouth (*Mylocheilus caurinus*), kokanee (*Oncorhynchus nerka*), northern squawfish (*Ptychocheilus oregonensis*), Dolly Varden (*Salvelinus malma*), and yellow perch (*Perca flavescens*).

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Because of the small size and abundance of the pygmy whitefish, it must be important as a primary carnivore available to species next in the food chain. The only extensive detailed publications on pygmy whitefish, however, are those of Eschmeyer and Bailey (1955) dealing with Lake Superior populations and of Heard and Hartman (1966) and McCart (1970) with Alaskan populations. Our work is concerned with populations from Flathead Lake and Bull Lake in the upper Columbia River drainage but involves comparisons where applicable to the Lake Superior and Alaskan forms. Some comparisons are also made with the mountain whitefish, *Prosopium williamsoni*, a closely related sympatric species.

ASSOCIATED FISHES AND DESCRIPTION OF THE LAKES

Flathead Lake is a large oligotrophic lake covering 126,000 surface acres and reaching a depth of 365 ft. Its major tributaries are the Flathead and Swan Rivers. Its outlet, the Flathead River, joins the Clark Fork River of the Columbia River.

Like many glacial lakes, Flathead Lake is depauperate in native fishes. Indigenous fishes in the lake are cutthroat trout (*Salmo clarki*), Dolly Varden, pygmy whitefish, mountain whitefish, longnose sucker (*Catostomus catostomus*), largescale sucker (*C. macrocheilus*), peamouth, redside shiner (*Richardsonius balteatus*), northern squawfish, and slimy sculpin (*Cottus cognatus*).

Around the turn of the century a number of other species were introduced. The exotic forms presently in the lake are rainbow trout (*Salmo gairdneri*), lake trout (*Salvelinus namaycush*), brook trout (*S. fontinalis*), kokanee, lake whitefish, black bullhead (*Ictalurus melas*), yellow perch, pumpkinseed (*Lepomis gibbosus*), and largemouth bass (*Micropterus salmoides*). Plants of other exotics, including a 1969 plant of coho salmon, *Oncorhynchus kisutch*, were not successful. The northern pike, *Esox lucius*, thrives in Flathead River below the hydroelectric dam at the lake's outlet but is not reported from the lake. Fish species most often taken in the same net settings with pygmy whitefish are lake whitefish, lake trout, and Dolly Varden.

Bull Lake is comparatively small and shallow and is somewhat eutrophic. The total surface is 1,250 acres and the maximum depth is 64 ft. Ross Creek, where the pygmy whitefish were captured during their spawning runs, is the largest tributary.

No thorough studies have been made of the fish species in Bull Lake but, besides pygmy whitefish, it is known to contain rainbow trout, cutthroat trout, brook trout, Dolly Varden, kokanee, mountain whitefish, redside shiner, northern squawfish, peamouth, longnose sucker, largescale sucker, largemouth bass, and a sculpin.

MATERIALS AND METHODS

Pygmy whitefish were collected from Flathead Lake during an investigation on fish populations by the Montana Fish and Game Department. A 35-ft former commercial fishing boat modified to handle specialized fishing gear and provided with a recording sonar was used to set and pull nets from 11 sample areas during 4 seasons from November 1967 through August 1971. Six hundred feet of gill netting ranging from ⅝-inch to 4-inch stretched mesh were laid in 165 settings. Except for spawning populations practically all pygmy whitefish were caught in the ⅝-inch and 1¼-inch mesh portion and were taken within 3 ft of the bottom. The largest collections were taken during the late summer at depths of 60 to 270 ft. Unfortunately, too few pygmy whitefish were taken to interpret an overall distributional pattern.

The Bull Lake collections were taken with seines from spawning aggregations in the lake's inlet during December of 1952, 1955, and 1967.

Counts on scales, gill rakers, and vertebrae followed the methods outlined by Hubbs and Lagler (1964). Gill raker counts included rudimentary rakers and sutures in the hypural complex were regarded as separating vertebrae. Specimens used for vertebral counts were eviscerated, filleted, cleared in KOH, and stained in alizarine red S according to the procedure of Evans (1948).

Standard lengths were measured in millimeters and weights in tenths of grams. To compare our results with the data of other authors who used fork length or total length, it was necessary to use conversion factors. Total length was considered equal to 0.21 plus 1.19 standard length, and the standard length equal to -0.09 plus 0.83 total length. The conversion of fork length to total length used was that given by Heard and Hartman (1966) where fork length times 1.0777 equals total length for specimens shorter than 100 mm and times 1.0845 for the larger specimens.

Scales for age and growth studies were removed from an area above the lateral line just posterior to the dorsal fin. Plastic impressions were made of the scales and projected to an enlargement of 67 times for measurement.

SOME MERISTIC CHARACTERS

Lateral-Line Scales

A striking character of the pygmy whitefish is its large scales. In its northern range the lateral-line scales number 50 to 73, in Lake Superior 54 to 62, in Flathead Lake 52 to 65, and Bull Lake 54 to 63 (Table 1). The mean number of scales varies somewhat among different populations. A low mean of 54.29 is given for fish from Chadburn Lake, Yukon, and a high of 71.57 for low-rakered fish from Lake Aleknagik (McCart, 1970). Pygmy whitefish from Flathead Lake and Bull Lake are intermediate. The closely related mountain whitefish possesses lateral-line scales ranging from 73 to 92 in the Columbia River drainage (Holt, 1960).

TABLE 1.—Frequency distribution of the lateral-line scale counts in pygmy whitefish.

Number of scales	Flathead Lake	Bull Lake
52	3	—
53	4	—
54	3	1
55	5	2
56	12	1
57	14	3
58	14	6
59	15	11
60	9	10
61	6	4
62	4	6
63	6	4
64	1	—
65	3	—
Mean	58.2	59.5

Gill Rakers

The number and length of gill rakers have proved useful in the systematics of coregonines. The range in gill rakers is considerable in pygmy whitefish, from 12 to 21. On the basis of gill raker number and other meristic and morphological data, McCart (1970) distinguished two forms of pygmy whitefish which occur sympatrically in some Alaskan lakes. One form has high raker counts and the other has low raker counts. McCart suggested a western refugium south of the ice sheet for the origin of the Alaskan low gill raker form, a Yukon-Bering Sea refugium for the Alaskan high gill raker form, and a Mississippian refugium for the Lake Superior form.

Pygmy whitefish from Flathead Lake have a range of 14 to 18 gill rakers (mean 15.83); those from Bull Lake range from 15 to 18 (mean 16.28). These means are considerably lower than the 18.28 mean of fish from Lake Superior (Table 2). According to McCart's figures, the Flathead Lake and Bull Lake populations would be classified as high-rakered in comparison with Lake Aleknagik populations,

TABLE 2.—Frequency distribution of gill raker counts in pygmy whitefish.

Locality	Number of gill rakers							
	14	15	16	17	18	19	20	Mean
Lake Superior[1]	—	—	1	6	17	13	3	18.28
Columbia River drainage:								
Lake McDonald[1]	—	2	5	5	3	5	—	17.20
Bull Lake[1]	—	2	6	10	2	1	—	16.71
Flathead Lake	4	15	24	8	3	—	—	15.83
Bull Lake	—	4	13	5	3	—	—	16.28
Alaska:								
Lake Aleknagik:[2]								
High raker			range 14-17					15.28
Low raker			range 12-15					13.46
Naknek Lake:[2]								
High raker			range 16-19					17.33
Low raker			range 13-16					14.54
Chignik Lake:[2]								
High raker			range 17-21					19.21
Low raker			range 13-16					14.16

[1] From Eschmeyer and Bailey (1955).
[2] From McCart (1970).

but intermediate compared to Naknek Lake and Chignik Lake populations. Our counts, as well as those on Lake McDonald fish, do not support McCart's contention that the low-rakered form persisted in the vicinity of the Columbia River Basin during the Pleistocene glaciation.

Vertebrae

As with other meristic characters, the vertebral count of the pygmy whitefish is low for a coregonine. The number of vertebrae is variable however—from 49 to 55. The plasticity of this character is within individual populations as the species exhibits similarity in the mean count of vertebrae throughout its range. The Flathead Lake fish have a mean number of 52.3 and the Bull Lake specimens, a mean of 52.7 (Table 3). Mean vertebral count of the fish from Lake Superior was given as 52.9 by Eschmeyer and Bailey (1955). The lowest mean is 51.5 for Chignik Lake (McCart, 1970).

It appears that most of the variation in the vertebral number is in the caudal rather than precaudal vertebrae. The number of caudal vertebrae ranges from 21 to 26 whereas the precaudals vary from 27 to 31 in Flathead Lake and Bull Lake fish. The number of caudals individually plotted with their respective total number have means that nearly increase by the value of one with each increase in similar value in total number of vertebrae (Table 4).

Although low, the total number of vertebrae of the pygmy whitefish overlaps the lower range of the mountain whitefish. Holt (1960) gave a range of 53 to 61 for the mountain whitefish in the Columbia River drainage. Twenty specimens of the mountain whitefish from Lolo Creek used in our study had caudal vertebrae ranging from 25 to 27, again a slight overlap.

TABLE 3.—Frequency distribution of total number of vertebrae in pygmy whitefish.

No. of vertebrae	Flathead Lake	Bull Lake
50	2	—
51	6	3
52	24	16
53	26	18
54	2	7
55	—	1
Mean	52.3	52.7

TABLE 4.—Relation of number of caudal vertebrae to total number of vertebrae in pygmy whitefish.

Item	Total vertebrae				
	51	52	53	54	55
Caudal vertebrae:					
Range	21-24	21-25	21-25	24-25	26
Mean	21.86	22.82	23.39	24.43	26.00
Number of specimens	7	33	33	7	1

AGE AND GROWTH

Age was determined for 494 pygmy whitefish taken from Flathead Lake during April 1967 through May 1971. Sex was determined on 272 specimens, mostly from mature fish captured in November and December.

Only one fish of age 0 was collected. Fish of this age are so small that they are unlikely to be captured in the collecting gear we used. The percentage of the total fish by age group was: 0, 0.2% ; I, 47.2% ; II, 46.1% ; III, 5.9% ; and IV, 0.6%. Overlap was considerable in the length-frequency distribution between adjacent age groups and between the sexes (Table 5).

Growth rate was calculated by establishing the relationship between the body length and the anterior scale radius. The value of 0.9854, the coefficient of variation r, developed on the 493 measurements, suggests a strong degree of linearity between the body-scale measurements. This linearity differs from the sigmoid body-scale relationship found for pygmy whitefish from Alaskan waters by Heard and Hartman (1966).

The equation fitted from the individual pairs of body and scale measurements was: Total body length = 0.913 anterior scale radius + 61.63. Mean body lengths from each scale radius were plotted against the calculated regression line shown in Figure 1. Total lengths were back calculated by direct proportion (Table 6).

Annual growth of females in Flathead Lake exceeded growth reported for Brooks Lake (Alaska), Lake McDonald (Montana), and Lake

TABLE 5.—Length frequency of age groups of pygmy whitefish from Flathead Lake, 1967-71.

[F, females; M, males.]

Total length	I		II		III		IV		Total	
(mm)	M	F	M	F	M	F	M	F	M	F
84	—	1	—	—	—	—	—	—	—	1
89	1	—	—	—	—	—	—	—	1	—
91	—	—	—	—	—	—	—	—	—	—
94	1	—	—	—	—	—	—	—	1	—
99	1	—	—	—	—	—	—	—	1	—
102	1	—	—	—	—	—	—	—	1	—
104	2	—	1	—	—	—	—	—	3	—
107	4	1	—	—	—	—	—	—	4	1
109	8	3	1	1	—	—	—	—	9	4
112	8	2	—	—	—	—	—	—	8	2
114	31	2	—	3	—	—	—	—	31	5
117	21	3	1	—	—	—	—	—	22	3
119	18	2	5	—	—	—	—	—	23	2
122	10	—	2	1	—	—	—	—	12	1
124	6	1	5	1	—	—	—	—	11	2
127	5	—	7	1	—	—	—	—	12	1
130	—	—	5	—	—	—	—	—	5	—
132	2	—	12	8	—	1	—	—	14	9
135	1	—	4	3	—	—	—	—	5	3
137	—	3	7	6	—	—	—	—	7	9
140	—	—	1	5	1	—	—	—	2	5
142	—	—	2	5	—	1	—	—	2	6
145	—	—	3	7	—	—	—	—	3	7
147	—	—	3	4	—	—	—	—	3	4
150	—	—	1	4	—	1	—	—	1	5
152	—	—	—	4	—	2	—	—	—	6
155	—	—	—	3	—	2	—	—	—	5
157	—	—	—	1	—	1	—	—	—	2
160	—	—	—	1	—	4	—	—	—	5
163	—	—	—	—	—	—	—	2	—	2
170	—	—	—	—	—	—	—	1	—	1
Mean length	116	116	129	140	132	153	—	165	121	138
Total number	120	18	60	58	1	12	—	3	181	91

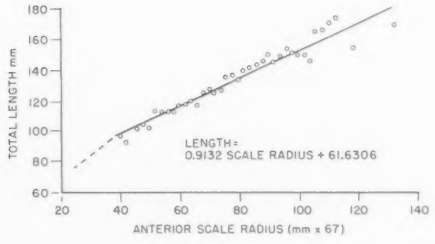

FIGURE 1.—Body length-scale radius relation of pygmy whitefish from Flathead Lake. Solid line is calculated equation; circles represent mean body lengths for given scale radii; dashed line connects estimated intercept at 25 mm length at scale formation.

Superior. Growth was nearly the same in Bull Lake. The initial growth of the Flathead Lake population was exceeded in Wood Lake, Alaska, and after the third year in MacLure Lake, British Columbia, where the fastest growth rate has been reported for the species (Figure 2).

Both Bull Lake and Flathead Lake collections indicate that few males live beyond their third growing year whereas some females reach the fifth growing year. Data from Wood River and the Naknek River systems in Alaska and from Lake Superior also show that females are longer lived. Females in Wood River can attain age VI and those in Lake Superior attain age VII.

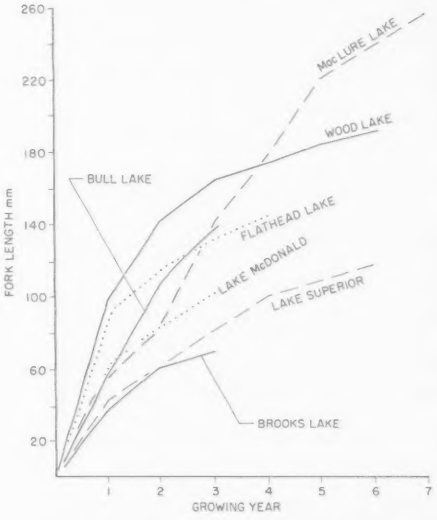

FIGURE 2.—Calculated growth of female pygmy whitefish from Flathead Lake compared with data from Bull Lake and Lake McDonald, Mont., and Lake Superior (Eschmeyer and Bailey, 1955); Wood Lake, Alaska (Rogers, 1964); Brooks Lake, Alaska (Heard and Hartman, 1966); and MacLure Lake, British Columbia (McCart, 1963).

FOOD HABITS

The importance of major food items of the pygmy whitefish of Flathead Lake shifts from month to month, undoubtedly according to availability. Chironomid larvae and pupae were the most important items consumed both by

TABLE 6.—Average calculated length and average length at capture of pygmy whitefish, from Flathead Lake, 1967-71.

[F, females; M, males; U, unknown sex.]

Age group	Sex	Number of fish	Average total length at capture (mm)	Calculated length at annulus formation			
				I	II	III	IV
0	U	1	79	—	—	—	—
I	M	120	117	100	—	—	—
	F	18	116	99	—	—	—
	U	95	110	95	—	—	—
II	M	60	128	98	116	—	—
	F	58	140	98	122	—	—
	U	110	134	101	123	—	—
III	M	1	140	100	124	142	—
	F	12	154	100	124	141	—
	U	16	150	101	122	137	—
IV	F	3	168	99	130	145	155
			Average increment				
	M	181	122	99	18	25	—
	F	91	138	98	24	20	13
	U	221	—	98	22	14	—
			Average length				
	M			99	117	142	—
	F			98	122	142	155
	U			98	123	137	—
	Combined			99	121	139	155

TABLE 7.—Percentage frequency of occurrence of food items in stomachs containing food and (in parentheses) percentage estimate of volume for pygmy whitefish from Flathead Lake.[1]

[The two percentage figures are the same or approximate because most stomachs contained only one kind of food.]

Food	May	June	July	Aug.	Sept.	Oct.	Nov.	Average
Cladocera: (including ephippia)	—	—	50 (50)	80 (80)	13 (15)	47 (48)	53 (56)	35
Diptera: Tendipedidae (chironomid larvae and pupae)	67 (67)	89 (95)	33 (37)	20 (20)	69 (71)	44 (45)	10 (8)	47
Trichoptera: (Hydroptilidae and Hydropsychidae)	11 (11)	4 (2)	2 (1)	—	3 (2)	—	—	3
Unknown insect parts	—	4 (2)	6 (4)	—	5 (4)	—	—	2
Fish eggs	—	—	—	—	—	—	6 (6)	1
Detritus and sand	22 (22)	3 (3)	9 (8)	—	10 (8)	9 (7)	31 (30)	12
Empty/full	3/12	0/27	14/68	1/6	5/44	12/44	26/77	61/278

[1] Items appearing in only one or two stomachs included: diatoms, copepods, Podocopa (Ostracoda), Mayfly nymphs (Ephemerotera), midge adults (Tendipedidae), leaf hopper (Cicadellidae), ants (Hymenoptera), terrestrial beattle (Coleoptera), and water mites (Hydracarina). All of these items composed only a small part of stomach contents.

volume and frequency of occurrence; cladocerans were close second (Table 7). No cladocera was consumed during May and June when chironomids were the main food source. Crustaceans became the prime food in July and August, but in September the reliance returned to dipterans. Cladocera apparently became more available in October and November and once more were the important source of food, particularly in November. Other foods were of minor importance during the months when stomachs were collected. The frequent presence of detritus and sand in the guts is evidence that this whitefish feeds at or near the bottom as visually confirmed by Heard and Hartman (1966).

Crustacea identified from the guts of pygmy whitefish from Flathead Lake included an ostracod; the cladocerans *Daphnia thorata*, *D. rosea*, *D. longiremis*, *Bosima longirostris*, and *Leptodora kindtii*; and the copepods *Diaptomus ashlandi*, *Epischura nevadensis*, and a cyclopoid copepod.

A December collection of spawning pygmy whitefish from Ross Creek demonstrates that these fish feed actively during their spawning period. Fish eggs, laid by fellow spawners, were the most frequently ingested food and made up by far the greatest volume. Chironomids were still taken in numbers, however, along with a few other insects (Table 8).

The feeding habits of this whitefish in other lakes are usually similar to those of fish in Flathead Lake. In Lake Superior, crustacea, mostly ostracods and amphipods, occurred in 95% of the stomachs. Chironomids were taken frequently but made up only 8% of the total volume. Fish eggs, presumably coregonine, occurred in collections of May and January (Eschmeyer and Bailey, 1955). Pygmy whitefish from a tributary of Lake Aleknagik, Alaska, fed on the larvae and pupae of chironomids (Rogers, 1964). In the Naknek River system the relative importance of food items differs between lakes. Chironomids accounted for 88% of the stomach volume in some lakes but only 5% in other waters. Plecopteran nymphs were important as food in some lakes or outlets. Periphyton never accounted for more than 4% of stomach contents. Fish eggs, probably from salmon, were taken in November (Heard and Hartman, 1966). Low-rakered Alaskan forms fed predominantly on bottom fauna and the high-rakered fish were almost exclusively plankton feeders (McCart, 1970).

TABLE 8.—Percentage frequency of occurrence of food items in stomachs containing food. Pygmy whitefish from Ross Creek during spawning run, 12 December 1967. The number of fish eggs eaten ranged from 1 to 21 per fish with an average of 6.

Cladocera	8
Diptera:	
Tendipedidae (chironomid larvae)	38
Ceratopogonidae larvae	3
Ephemeroptera:	
Heptagenia nymph	3
Unknown insect remains	8
Fish eggs	75
Detritus and sand	33
Empty stomachs	9 of 50

REPRODUCTION

Age and Size at Maturity

Collections of pygmy whitefish were made from the inlet of Bull Lake during the spawning runs in December of three different years. Only the last collection (1967) included a large number of fish—280, all but 4 were males. The predominance of males in the three collections may be explained by the earlier arrival of males to the spawning aggregation. None of the gonads examined was spawned out.

In the three combined collections, 50% of the males were in their second growing season (age I), 47% at age II, and only 3% at age III. In the small sample of females, none was age I, 64% were age II, and 36% were age III. Except for one large male with three annuli, the females were consistently larger than the males in each age group (Table 9). The smallest ripe male was 86 mm standard length and the largest was 130 mm; the smallest female was 120 mm and the largest was 139 mm.

In late November and December large numbers of pygmy whitefish move from the deep water of Flathead Lake and congregate at the mouths of the Swan and Flathead Rivers before they enter the river systems presumably to spawn. The males outnumber the females 6.7:1 in these concentrations. Of the age I males,

TABLE 9.—Frequency distribution according to standard length of three age groups of ripe pygmy whitefish taken from Ross Creek in three different years.

Sex and standard length (mm)	2 Dec. 1952		10 Dec. 1955			20 Dec. 1967		
	I	II	I	II	III	I	II	III
Males:								
86- 90	4	—	—	—	—	2	—	—
91- 95	4	—	16	—	—	4	—	—
96-100	2	2	7	—	—	4	1	—
101-105	—	5	1	5	—	—	2	—
106-110	—	4	—	12	—	—	8	—
111-115	—	—	—	2	—	—	—	—
116-120	—	—	—	—	2	—	—	—
126-130	—	—	—	—	—	—	—	1
Females:								
116-120	—	1	—	—	—	—	—	—
121-125	—	—	—	1	—	—	1	—
126-130	—	1	—	2	—	—	—	—
131-135	—	—	—	1	1	—	—	2
135-140	—	—	—	—	—	—	—	1

74.5% were sexually mature. All males age II or older were mature. As in the Bull Lake population, the females mature more slowly than the males. The percentage maturity of the females was 27.8 at age I, 90.2% at age II, and 100% for older fish. Younger breeding age in the males and the larger size of mature females characterize the other widely separated populations (Eschmeyer and Bailey, 1955; Heard and Hartman, 1966).

Female pygmy whitefish obviously spawn in consecutive years. Mature ripe eggs were present in the abdominal cavity while smaller eggs, 1 mm in diameter, were developing in the ovaries of ages II and III females.

Sex Ratio

The predominance of males in Bull Lake collections has been discussed previously. Although variable from sample to sample the sex ratio of all pygmy whitefish taken from Flathead Lake in 1969 was nearly equal (Table 10). When collections for 1967 through 1971 were combined, however, males exceeded females by a ratio of 2:1 (Table 5). The sexes were about equal at age II but many more males were taken at age I.

Fecundity

The fecundity of individual fish from Lake Superior and Alaska varied widely. In Flathead Lake egg counts of 28 females ranged from 156 to 918 and averaged 588. The larger fish tended generally to have the most eggs, but exceptions were frequent (Table 11). Four large spawners from Bull Lake had from 1,027 to 1,136 eggs. In Lake Superior egg counts ranged from 93 to 597 and averaged 362 (Eschmeyer and Bailey, 1955); those from the Naknek River system ranged from 103 to 1,153 (Heard and Hartman, 1966).

Conversion of our lengths to total lengths in inches and comparison with Eschmeyer and Bailey's length-fecundity curve shows that pygmy whitefish from Flathead Lake produce more eggs for their size than do the Lake Superior fish and that those from Bull Lake are even more productive. Fish from Bull Lake with total lengths from 6.0 to 6.5 inches have egg counts slightly more than 1,000 compared with about 650 for the Lake Superior fish. If the length-fecundity curve of Heard and Hartman is projected, the Bull Lake population was about the same as fish from South Bay in the Naknek River system, but the Flathead fish produced fewer eggs. Fish in the 5.4- to 5.7-inch range from Flathead Lake had 560 eggs whereas those from South Bay had about 700 eggs. Heard and Hartman explained the differences in fecundity among populations as adaptations to different environmental conditions that produce higher or lower survival opportunities for the species.

TABLE 10.—Length and weight of pygmy whitefish from Bull Lake and Flathead Lake.

[Ranges in parentheses.]

Locality	Number of fish	Sex	Standard length (mm)	Weight (g)
Ross Creek:				
10 Dec. 1955	45	male	102 (90-120)	15.8 (10.3-25.0)
	5	female	130 (125-135)	39.6 (30.7-44.0)
12 Dec. 1967	53	male	107 (90-130)	20.7 (9.3-27.5)
	17	female	137 (125-160)	36.0 (26.8-55.6)
Flathead Lake:				
May-Nov. 1969	102	male	99 (75-116)	11.8 (4.8-22.8)
	117	female	109 (70-140)	18.0 (3.0-42.6)

TABLE 11.—Production of eggs of pygmy whitefish.

Locality	Number of fish	Average weight (g)	Range in standard length (mm)	Number of eggs	
				Range	Mean
Bull Lake	4	43.5	130-135	1,027-1,136	1,084
Flathead Lake	5	16.7	107-110	414-700	547
	11	20.7	111-120	227-733	558
	10	24.9	122-133	156-918	564

Time and Locality of Spawning

No fully mature pygmy whitefish has been found in Bull Lake in November, but ripe fish were readily collected from Ross Creek, the inlet, on 26 December and 12 January 1952, 10 December 1955, and 20 December 1967. Also, fisherman were observed catching ripe fish from the mouth of Stanley Creek, a tributary at the opposite end of the lake, on 3 January 1952 (Weisel and Dillon, 1954). Although milt and roe were easily stripped, the appearance of the gonads indicated that most of the fish had not spawned. The spawning period in Bull Lake must extend from mid-December well into January. All evidence indicates pygmy whitefish spawn in streams rather than in the lake. As previously stated, mature fish were congregated at the mouths of the two major inlets of Flathead Lake in late November and December.

The species spawns in Alaska apparently between mid-November and mid-December in rivers and at the mouths of rivers during the night. In Lake Superior, Glacier National Park, and British Columbia the fish is believed to spawn in November or December in shallow water.

DISCUSSION

The pygmy whitefish is typified by low meristic counts. In gill raker counts the populations from Flathead and Bull Lakes are intermediate compared to Alaskan populations. This does not support McCart's (1970) contention that the low-rakered form persisted in the Columbia River Basin during Pleistocene glaciation. Vertebral counts range widely even within individual populations. Most of the vertebral variation is in the caudal rather than in the precaudal vertebrae.

The pygmy whitefish is flexible in diet and feeding behavior. Depending on the season and locality, the species may feed primarily on insects and zooplankton or on macrobenthic crustaceans. In any one habitat, however, the diet is either highly selective or restricted compared to many other species of fishes.

The pygmy whitefish must be important in the trophic system of Flathead Lake. They are a small, abundant primary carnivore and consequently must be an important food source for the secondary carnivores such as lake trout and Dolly Varden which frequent the deeper water. Its primary food competitor is undoubtedly the lake whitefish. The lake whitefish feeds extensively on molluscs but also includes chironomids and copepods as main dietary items in Flathead Lake (Brunson and Newman, 1951).

The species is short-lived. In the Montana populations no male was found older than age III and no female beyond age IV. In growth rate and fecundity the Montana populations are similar to those from Alaska and Lake Superior.

The pygmy whitefish exists successfully with sympatric salmonoids in spite of its small size and relatively low egg production. The mountain whitefish in Montana, its closest rival in respect to reproduction, produces an average of 4,400 eggs; the largest pygmy whitefish produces a quarter of this number. However the pygmy whitefish produces more eggs per pound of fish—10,000 eggs for Bull Lake specimens compared with 5,340 for mountain whitefish (Brown, 1952). This production is made possible by the reduced size of the eggs of the pygmy whitefish, which are 2.4 to 2.6 mm in diameter when water hardened compared with

3.1 to 4.2 mm for mountain whitefish. Booke (1970) postulated that the large-egg coregonine species gave rise to small-egg types. He admitted that the small-egg size of the pygmy whitefish does not fit his hypothesis because the species is considered to be the most primitive of the subfamily Coregoninae but that this may be a specialized character; and if the pygmy whitefish had the growth potential of the other species in the genus, it would probably have a larger egg. Also compensating for the low egg number per female, the pygmy whitefish spawns at an earlier age. Most mountain whitefish do not mature until their third or fourth year (Sigler, 1951; Brown, 1952), 1 to 2 years later than female pygmy whitefish and 2 years later than male pygmy whitefish. The early maturation and shorter life span of the male pygmy whitefish ensures greater fecundity and abundance of the species at lower consumption of food.

Evidence suggests strongly that direct competition between the two whitefish species on the spawning grounds is avoided by a difference in spawning time. Booke (1970) noted that large-egg coregonines spawn earlier than those with small eggs. From the information available, it appears that in Montana the large-egg mountain whitefish spawns about a month earlier than the small-egg pygmy whitefish.

The small size and consequential small egg diameter of the pygmy whitefish may be explained by the rigors of the glacial period. The known range of the species is restricted to recently glaciated areas. During the glacial period it probably retreated less than other coregonines from the glacial margins. The small size and early spawning age were very possibly adaptations for survival in cold and nutrient-poor waters.

LITERATURE CITED

BOOKE, H. E.
1970. Speciation parameters in coregonine fishes: I. Egg-size II. Karyotype. *In* C. C. Lindsey and C. S. Woods (editors), Biology of corgonid fishes, p. 61-66. Univ. Manit. Press, Winnipeg.

BROWN, C. J. D.
1952. Spawning habits and early development of the mountain whitefish, *Prosopium williamsoni*, in Montana. Copeia 1952:109-113.
1971. Fishes of Montana. Big Sky Books, Mont. State Univ., Bozeman, 207 p.

BRUNSON, R. B., AND H. W. NEWMAN.
1951. The summer food of *Coregonus clupeaformis* from Yellow Bay, Flathead Lake, Montana. Proc. Mont. Acad. Sci. 10:5-7.

ESCHMEYER, P. H., AND R. M. BAILEY.
1955. The pygmy whitefish, *Coregonus coulteri*, in Lake Superior. Trans. Am. Fish. Soc. 84:161-199.

EVANS, H. E.
1948. Clearing and staining small vertebrates in toto, for demonstrating ossification. Turtox News 26:42-47.

HEARD, W. R., AND W. L. HARTMAN.
1966. Pygmy whitefish *Prosopium coulteri* in the Naknek River system of southwest Alaska. U.S. Fish and Wildl. Serv., Fish. Bull. 65:555-579.

HOLT, R. D.
1960. Comparative morphometry of the mountain whitefish (*Prosopium williamsoni*). Copeia 1960: 192-200.

HUBBS, C. L., AND K. F. LAGLER.
1964. Fishes of the Great Lakes Region. Univ. Mich. Press, Ann Arbor, 213 p.

MCCART, P. J.
1963. Growth and morphometry of the pygmy whitefish (*Prosopium coulteri*) in British Columbia. M.S. Thesis, Univ. British Columbia, Vancouver, 97 p.
1970. Evidence for the existence of sibling species of pygmy whitefish (*Prosopium coulteri*) in three Alaskan Lakes. *In* C. C. Lindsey and C. S. Woods (editors), Biology of coregonid fishes, p. 81-98. Univ. Manit. Press, Winnipeg.

ROGERS, D. E.
1964. Some morphological and life history data on pygmy whitefish from Wood River. *In* Research in fisheries . . . 1963, p. 24-25. Coll. Fish., Fish. Res. Inst., Univ. Wash., Contrib. 166.

SCHULTZ, L. P.
1941. Fishes of Glacier National Park, Montana. U.S. Fish Wildl. Serv., Cons. Bull. 22, 42 p.

SIGLER, W. F.
1951. The life history and management of the mountain whitefish *Prosopium williamsoni* (Girard) in Logan River, Utah. Utah State Agric. Coll., Bull. 347:1-21.

WEISEL, G. F., AND J. B. DILLON.
1954. Observations on the pygmy whitefish, *Prosopium coulteri*, from Bull Lake, Montana. Copeia 1954:124-127.

NOTES

OCCURRENCE OF MATURE REDFISH, *SEBASTES MARINUS*, IN SPORT FISHERY OF THE NEW YORK BIGHT

In the 1971 sport fishery survey of the New York Bight waters, party boat captains reported catching redfish, *Sebastes marinus*, along the edges of the Hudson Canyon. Specimens obtained and examined later were found to be sexually mature fish. This is the first record of redfish being caught in the marine sport fishery off New York, and is a substantial extension of the southern and western breeding range for *Sebastes* in the north Atlantic.

Redfish occur on both sides of the north Atlantic and Goode and Bean (1895) listed the southernmost limit in the western Atlantic off the northern coast of New Jersey (lat 39°48′N; long 71°49′W). Schroeder (1955) reiterated this limit when he reported catching redfish between long 70°00′W and 71°59′W in water deeper than 394 m. Davis and Joseph (1964) reported one specimen (330 mm SL) off Virginia (lat 37°38′N; long 74°15′W) but did not include details on maturation. Prior to my find, the southernmost extent of a breeding population in the western Atlantic was that reported by Bigelow and Schroeder (1953) from Great South Channel off Nantucket Island.

Redfish exist in commercial concentrations from the Gulf of Maine and Georges Bank north to southern Greenland. Although an excellent table fish, redfish are not actively sought by New England anglers because they are usually found in deep water and provide little sporting action. They are caught regularly by anglers at Eastport, Maine (Kelly and Barker, 1961) and occasionally elsewhere along the Maine coast, but few are caught by sportsmen south of there.

During July and August 1971, I collected 14 specimens (13 ripe males and 1 gravid female containing well-developed larvae) from party boat captains. These redfish had an average length of 208 mm, ranging from 188 to 222 mm and averaged 257 g, ranging from 190 to 309 g. Ages ranged from 7 to 11 years with 8-year-old fish being the dominant age group. Their physical characteristics are like those described and pictured by Bigelow and Schroeder (1953) for *Sebastes marinus* from the Gulf of Maine. Each fish had a well-developed bony protuberance on the lower jaw and the anterior preopercular spine projected anteroventrally (Figure 1). The average ratio of horizontal diameter of orbit to head length was 29.5%.

Party boat captains caught these specimens incidentally while fishing for red hake, *Urophycis chuss*; tautog, *Tautoga onitis*; and black sea bass, *Centropristis striata*; on wrecks in 55 to 69 m in the upper end of the Hudson Canyon (general area: lat 40°12′N; long 73°44′W) (Figure 2). Party boat captains also reported

FIGURE 1.—A mature male redfish, 222 mm SL, caught at the northern end of the Hudson Canyon.

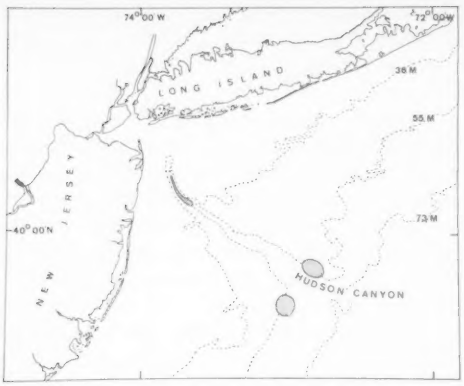

FIGURE 2.—The three areas (cross hatch) where sport fishermen caught redfish in the New York Bight.

catching redfish while fishing for Atlantic cod, *Gadus morhua*, and pollock, *Pollachius virens*, on wrecks deeper than 55 m in the general vicinities of lat 39°48′N, long 72°50′W and lat 39°36′N, long 73°03′W (Figure 2). I did not inspect these fish for positive identification. I received no reports of redfish being caught in water shallower than 55 m or any reports of redfish being caught over natural habitats. Party boat captains reported catching redfish during February, March, June, July, and August, mostly during the latter 2 months.

Several party boat captains reported catching redfish during the last 10 years. Although some captains said they caught up to 35 redfish during at least one trip in past years, I estimate that the total sportsmen's catch in 1971 was less than 100 fish.

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Literature Cited

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

DAVIS, J., AND E. JOSEPH.
1964. Southern record of *Sebastes marinus*, ocean perch. Chesapeake Sci. 5(4):212.

GOODE, G. B., AND T. H. BEAN.
1895. Oceanic ichthyology. U.S. Natl. Mus., Spec. Bull. 2, 553 p.

KELLY, G. F., AND A. M. BARKER.
1961. Observation on the behavior, growth, and migration of redfish at Eastport, Maine. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer. 150:263-275.

SCHROEDER, W. C.
1955. Report on the results of exploratory otter-trawling along the continental shelf and slope between Nova Scotia and Virginia during the summers of 1952 and 1953. Pap. Mar. Biol. Oceanogr., Deep-Sea Res., Suppl. 3:358-372.

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OPTIMUM LIGHT AND TEMPERATURE REQUIREMENTS FOR *GYMNODINIUM SPLENDENS*, A LARVAL FISH FOOD ORGANISM[1,2]

In recent years, it has been possible to substitute the marine dinoflagellate *Gymnodinium splendens* for wild natural plankton as a food source for first-feeding larval anchovies, *Engraulis mordax* (Lasker et al., 1970). *G. splendens* is ideal for this larval marine fish at this developmental stage because the alga's size (approximately 53 μm diameter) is similar to the size range of natural food particles. Reasonably lengthy larval survival (up to 19 days) can be achieved in the laboratory by first using this dinoflagellate and later supplementing with veligers (Lasker et al., 1970). The alga has also been used in combination with the rotifer *Brachionus plicatilis* as a larval food source (Theilacker and McMaster, 1971).

These developments have made possible new studies of anchovy larval behavior (Hunter, 1972) and nutrition (Conklin, unpublished data). Furthermore, the use of *G. splendens* may be of help in rearing other larval fish.

G. splendens is easily grown in an enriched seawater medium that was developed by Sweeney (1951, 1954) and Sweeney and Hastings (1957). The organism was first cultured with soil extract in the medium (Sweeney, 1951) which was later replaced with vitamin B_{12} (Sweeney, 1954). However, for routine culturing soil extract suffices and also provides trace metals and unknown organic factors.

The dinoflagellate has been cultured at 16°C and a light intensity of 60-70 footcandles (Sweeney, 1951); at 20°C and 200-400 footcandles (Sweeney, 1954) and at 20°C and 500 footcandles (Lasker et al., 1970), but optimum physical conditions for growth were not determined. Such information would be of value in setting up continuous cultures of *G. splendens* or in further improving conditions for mass cultures. The purpose of this paper is to establish the optimum conditions of light and temperature for *G. splendens* culture—conditions that result in a maximum growth rate.

Materials and Methods

Our culture of *G. splendens* was isolated from a water sample taken from the Scripps Institution pier in March 1969. It is unialgal but not bacteria-free. *Gymnodinium* is maintained in the enriched seawater medium of Sweeney and Hastings (1957) plus the Fe solution of Rodhe (1948). One liter of medium contains 750 ml seawater, 10 ml 0.1% EDTA (disodium ethylenedinitrilo tetra-acetate), 2 ml 1 M KNO_3, 2 ml 0.1 M K_2HPO_4, 20 ml of soil extract (prepared by autoclaving equal weights of untilled loam and glass distilled water followed by filtration through Whatman[3] No. 4 paper), 0.25 ml Rodhe Fe solution (prepared by dissolving 1.33 g ferric citrate and 1.33 g citric acid in 100 ml of double distilled water) and 216 ml (glass) distilled water. Autoclaving the medium results in a precipitate, which can be avoided by sterile filtration. Stock cultures of *G. splendens* were maintained at 500 footcandles (5,000 lux) and 21°C.

Experimental cultures were grown in this same medium. Cells were concentrated from exponentially growing stock cultures by gentle reverse filtration (Dodson and Thomas, 1964) and inoculated into 65-ml bottles containing 50 ml of medium to give an initial cell count of 200-500 cells/ml.

The culture bottles were then placed in temperature gradient block A of Thomas, Scotten, and Bradshaw (1963). This apparatus consisted of an aluminum block containing 30 holes. Prior to starting the experiment, thermostatted cold water was pumped through one end of the block and warm water was pumped through the other end. This set up a thermal gradient so that there were six rows

[1] Contribution from the Scripps Institution of Oceanography.

[2] This work was part of the STOR (Scripps Tuna Oceanography Research) Program. It was supported by the Oceanography Section, National Science Foundation Grant No. GA-32529X and by Marine Research Committee (California Department of Fish and Game) Grant No. M-13 to Reuben Lasker. The work was performed in the Southwest Fishery Center, National Marine Fisheries Service, NOAA.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

of five holes each at a given temperature. The bottles were illuminated from below through plastic windows in each hole. The continuous fluorescent light was attenuated with fogged photographic film filters placed below each window. Thus, at each of six temperatures, five light intensities were achieved. The light intensity in each hole was measured by an International Rectifier I2BM silicon photocell which was calibrated against a Weston Model 756 footcandle meter and an Eppley radiometer using the same fluorescent light source.

Counts of cells in each culture were made at daily intervals by taking 1-ml aliquots and counting all the cells in a 0.1-ml portion using a Palmer-Maloney counting chamber. Cell numbers were plotted against time in days on semilogarithmic paper. Growth rates during the exponential phase of growth were calculated by the equation:

$$\mu_2 = \frac{\log_2 N_2 - \log_2 N_1}{t_2 - t_1}$$

where N_1 and N_2 are cell counts at times t_1 and t_2. μ_2 is expressed as doublings of cell numbers per day.

Results and Discussion

Three experiments were performed. The first two were terminated after only 4 days of growth because of failure of the temperature-controlling equipment and because of contamination of some of the cultures with a small, colorless flagellate. Nevertheless, these preliminary experiments served to establish that growth of *G. splendens* was optimum at moderate temperatures and light intensities.

This result was confirmed in the third experiment in which growth was followed for 8 days. Figure 1 shows the growth rates that were achieved during the exponential phase of growth at different temperatures and intensities in this experiment. No growth occurred at 10° and 30°C and was suboptimal at 15°C. Growth was maximal at 20-27°C and at a light intensity of 2-9 kilolux. These are rather wide ranges of

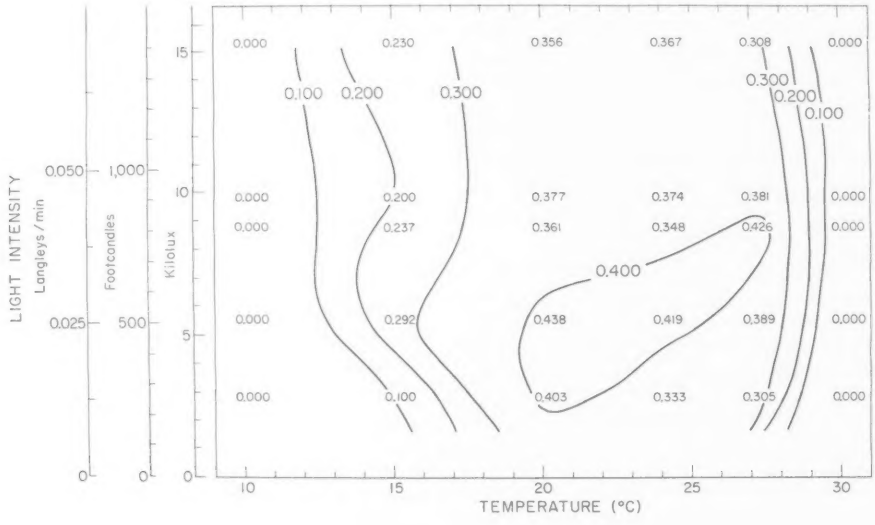

FIGURE 1.—Growth rates of *Gymnodinium splendens* at various light intensities and temperatures. The numbers are rates in doublings per day at each intensity and temperature and the data are also contoured to show similar rates.

TABLE 1.—Optimum temperatures and light intensities for growth of marine dinoflagellates.

Organism	Optimum temperature range (°C)	Optimum light intensities (kilolux)	(ly/min)	Reference
Peridinium sp.	18-20	—	>0.023	Barker (1935)
Prorocentrum micans	25	—	>0.023	Barker (1935)
Prorocentrum micans	—	>6	>0.03	Kain and Fogg (1960)
Prorocentrum gracile	18	—	>0.023	Barker (1935)
Amphidinium carteri	20-30	—	0.1-0.4	Jitts et al. (1964)
Gonyaulax polyedra	25	5-10	—	Hastings and Sweeney (1964) Sweeney (unpublished data)
Gymnodinium simplex	23-28	6-20	—	Thomas (1966)
Gymnodinium splendens	20-27	2-9	0.01-0.04	This paper

temperature and light, but it was surprising that rates were reduced slightly at higher light intensities.

Optimum temperatures and intensities for some other marine dinoflagellates are given in Table 1. *G. splendens* has temperature optima that are close to those of other dinoflagellates, but its light intensity requirements are somewhat lower.

These results are useful in providing proper conditions for mass cultures. Normal room temperatures are proper and optimum light intensities (about 5 kilolux) can be provided with banks of 40-W fluorescent lights placed about 5-10 cm away from culture flasks. At a growth rate of 0.4 doublings per day, a culture inoculated with a few hundred cells per milliliter will increase 10 fold in about 8 days.

Literature Cited

BARKER, H. A.
1935. The culture and physiology of the marine dinoflagellates. Arch. Mikrobiol. 6:157-181.

DODSON, A. N., AND W. H. THOMAS.
1964. Concentrating plankton in a gentle fashion. Limnol. Oceanogr. 9:455-456.

HASTINGS, J. W., AND B. M. SWEENEY.
1964. Phased cell division in the marine dinoflagellates. *In* E. Zeuthen (editor), Synchrony in cell division and growth, p. 307-321. John Wiley, N.Y.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

JITTS, H. R., C. D. MCALLISTER, K. STEPHENS, AND J. D. H. STRICKLAND.
1964. The cell division rates of some marine phytoplankters as a function of light and temperature. J. Fish. Res. Board Can. 21:139-157.

KAIN, J. M., AND G. E. FOGG.
1960. Studies on the growth of marine phytoplankton. III. *Prorocentrum micans* Ehrenberg. J. Mar. Biol. Assoc. U.K. 39:33-50.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

RODHE, W.
1948. Environmental requirements of freshwater plankton algae. Symb. Bot. Ups. 10:1-149.

SWEENEY, B. M.
1951. Culture of the dinoflagellate Gymnodinium with soil extract. Am. J. Bot. 38(a):669-677.
1954. Gymnodinium splendens, a marine dinoflagellate requiring vitamin B_{12}. Am. J. Bot. 41:821-824.

SWEENEY, B. M., AND J. W. HASTINGS.
1957. Characteristics of the diurnal rhythm of luminescence in Gonyaulax polyedra. J. Cell. Comp. Physiol. 49:115-128.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

THOMAS, W. H.
1966. Effects of temperature and illuminance on cell division rates of three species of tropical oceanic phytoplankton. J. Phycol. 2:17-22.

THOMAS, W. H., H. L. SCOTTEN, AND J. S. BRADSHAW.
1963. Thermal gradient incubators for small aquatic organisms. Limnol. Oceanogr. 8:357-360.

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ERRATA

Fishery Bulletin, Vol. 71, No. 1

HIDA THOMAS S., "Food of tunas and dolphins (Pisces: Scombridae and Coryphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri* (Engraulidae)," p. 135-143.

1) Page 139, right column, line 1, correct line to read:
Majuro and Arno Atolls in February 1972 were feed-

LINDALL, WILLIAM N., JR., JOHN R. HALL, AND CARL H. SALOMAN, "Fishes, macroinvertebrates, and hydrological conditions of upland canals in Tampa Bay, Florida," p. 155-163.

1) Page 158, left column, line 12, delete:
linity at the control station was 9.0‰ higher than

PRISTAS, PAUL J., AND RANDALL P. CHEEK, "Atlantic thread herring (*Opisthonema oglinum*) - movements and population size inferred from tag returns," p. 297-301.

1) Page 300, right column, line 3 and subsequent lines in this paragraph, correct lines to read:
of the population. This effect would produce an underestimate of the stock size. On the other hand, this calculation might overestimate population size because we were unable to determine rate of recruitment and no adjustment has been made for tag loss due to shedding or mortality.
2) Page 301, left column, first author line, correct line to read:
PAUL J. PRISTAS[2]

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